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Fungal evolution: diversity, taxonomy and phylogeny of the Fungi

Miguel A. Naranjo-Ortiz[1] and Toni Gabaldón[1,2,3,*,†]

[1] *Bioinformatics and Genomics Programme, Centre for Genomic Regulation (CRG), The Barcelona Institute of Science and Technology, Dr. Aiguader 88, Barcelona 08003, Spain*
[2] *Health and Experimental Sciences Department, Universitat Pompeu Fabra (UPF), 08003 Barcelona, Spain*
[3] *ICREA, Pg. Lluís Companys 23, 08010 Barcelona, Spain*

ABSTRACT

The fungal kingdom comprises a hyperdiverse clade of heterotrophic eukaryotes characterized by the presence of a chitinous cell wall, the loss of phagotrophic capabilities and cell organizations that range from completely unicellular monopolar organisms to highly complex syncitial filaments that may form macroscopic structures. Fungi emerged as a 'Third Kingdom', embracing organisms that were outside the classical dichotomy of animals *versus* vegetals. The taxonomy of this group has a turbulent history that is only now starting to be settled with the advent of genomics and phylogenomics. We here review the current status of the phylogeny and taxonomy of fungi, providing an overview of the main defined groups. Based on current knowledge, nine phylum-level clades can be defined: Opisthosporidia, Chytridiomycota, Neocallimastigomycota, Blastocladiomycota, Zoopagomycota, Mucoromycota, Glomeromycota, Basidiomycota and Ascomycota. For each group, we discuss their main traits and their diversity, focusing on the evolutionary relationships among the main fungal clades. We also explore the diversity and phylogeny of several groups of uncertain affinities and the main phylogenetic and taxonomical controversies and hypotheses in the field.

Key words: Fungi, taxonomy, phylogeny, phylogenomics, diversity.

CONTENTS

* Author for correspondence (Tel: +34 933160281; E-mail: toni.gabaldon.bcn@gmail.com)
† Present address: Comparative Genomics Group Barcelona Supercomputing Centre (BSC-CNS), and Institute for Research in Biomedicine (IRB), Barcelona, Spain.

I. INTRODUCTION

If we were to review the most recent advances in animal or plant phylogeny and taxonomy, a paragraph detailing the relevance of any of those groups would be superfluous. Animals and plants are studied not only in specialized biology degrees, but even in primary education. Fungi, though, only merit a brief mention in high school text books, and very rarely occupy a central position in university-level biology degrees, generally falling between the fields of botany and microbiology (Editorial, 2017; Freimoser, 2017). Yet Fungi are literally everywhere, shaping the world as we know it. They can be found in the stratosphere (Wainwright, Wickramasinghe, & Rajaratnam, 2003) and the bottom of the Dead Sea (Oren & Gunde-Cimerman, 2012), from antarctic glaciers (Freeman *et al.*, 2009) to torrid deserts (Gonçalves *et al.*, 2016), from the gut of flies (Blackwell, 2017) to deep oceanic sediments (Nagahama *et al.*, 2011), and anywhere in between. Fungi are powerful players in global bio-geochemistry, recycling carbon and mobilizing nitrogen, phosphorus and other bio-elements. They provide essential support to plant life in the form of endophytes and mycorrhizae, while fungal pathogens can decimate plant and animal populations, threatening food supplies and even pushing some species to the brink of extinction. The metabolic singularities of many fungi have provided humanity with fermented foods and beverages to feed us and delight our senses, medicines to cure our bodies, and many compounds with important industrial usages. Fungi themselves are an important and valued source of food, and in the near future fungal biomass might even help to clothe and shelter us (Wojciechowska, 2017; Jones *et al.*, 2018).

Fungal taxonomy has undergone major changes since the recognition of this group in Linnean taxonomy, where it was considered part of the 'Regnum Vegetabile' (Linnaeus, 1767). Early classifications included several groups of heterotrophic eukaryotes characterized by their osmotrophic nutrition with diverse phylogenetic affinity, as well as a core of clades collectively deemed the 'true fungi', or Eumycota (Whittaker, 1969). True fungi generally share the following traits: (*i*) the presence of a β-glucan and (generally) chitin cell wall, at least in their spores; (*ii*) they are usually unicellular, or grow as a mycelium – a multinucleated, walled, cylindrical cell of variable size; (*iii*) the presence of the amino adipidic pathway for the biosynthesis of lysine; and (*iv*) the presence of flattened mitochondrial crystae (Adl *et al.*, 2012, 2018). Nevertheless, numerous exceptions exist for virtually all these traits, both in the form of secondary losses within fungi, as well as by their presence in other eukaryotic groups (Richards, Leonard, & Wideman, 2017). Early on, four major phyla were defined within the true fungi, based on their morphological and reproductive traits: Chytridiomycota, Zygomycota, Ascomycota and Basidiomycota (Whittaker, 1969). Later, molecular phylogenies proved the paraphyly of Zygomycota and Chytridiomycota (Tanabe, Watanabe, & Sugiyama, 2005; James *et al.*, 2006*a*,*b*, White *et al.*, 2006), as well as the affinity of Microsporidia and the chytrid-like *Rozella* to the fungal kingdom (Keeling, Luker, & Palmer, 2000; Fischer & Palmer, 2005; James *et al.*, 2006*b*). More recently, the advent of environmental-sequencing-based technologies have brought about the recognition of a novel highly diverse and cosmopolitan clade of fungal-like organisms that include *Rozella* and some related genera, for which the terms Rozellidea, Rozellomycota and Cryptomycota have been used (Lara, Moreira, & López-García, 2010; Jones *et al.*, 2011; Adl *et al.*, 2012; James & Berbee, 2012; Corsaro *et al.*, 2014*b*). Finally, the Aphelidea, a poorly studied clade of amoeboid parasitoids of unicelular algae

was found to be sister group to Microsporidia and *Rozella*, completing the fungal family portrait (Karpov *et al.*, 2014*a*).

The most up-to-date taxonomy comprises the described diversity of known true fungi, dividing it into nine major lineages: Opisthosporidia, Chytridiomycota, Neocallimastigomycota, Blastocladiomycota, Zoopagomycota, Mucoromycota, Glomeromycota, Ascomycota and Basidiomycota. Together, these lineages form a monophyletic clade, the true fungi (Fig. 1), which is sister to a group of amoeboid protozoans consisting of the Nucleariida (*Nuclearia*, *Micronuclearia*, *Parvularia*) and Funticulida (*Fonticula*) (Karpov *et al.*, 2014*a*; Spatafora *et al.*, 2017*a*; Tedersoo *et al.*, 2018). Below, we describe the main features of these nine fungal lineages, plus several other groups that might represent additional independent lineages or whose affinity to any of the well-defined groups is still not fully resolved.

II. ZOOSPORIC FUNGI

All Fungi must descend from an organism that was single celled and, at least at some point in its life cycle, able to swim with the use of posterior flagella. Several fungal lineages still present this lifestyle, although in some cases secondary loses have occurred. The evolutionary relationships among these lineages remain unresolved, mostly due to the deep divergence of these lineages, the current incomplete sampling, and the parasitic nature of many. Figure 2 illustrates some of these organisms, and the main lineages are listed in Table 1.

(1) Opisthosporidia

This group is formed by three main lineages: Aphelidea, Rozellidea and Microsporidia (also known as the ARM clade). All known species in this clade are intracellular parasites or parasitoids of a wide range of eukaryotes. The term Cryptomycota was proposed to describe a series of cosmopolitan aquatic organisms related to *Rozella* and to highlight an apparent diversity comparable to that of known fungi (Jones *et al.*, 2011). We herein use the term Rozellidea to describe *Rozella* and related environmental sequences and discard the use of Cryptomycota henceforth. The inclusion of Aphelidea created the Opisthosporidia (Karpov *et al.*, 2014*a*). However, some phylogenetic studies suggest that Opisthosporidia are paraphyletic, with Rozellidea + Microsporidia as the earliest splitting branch, followed by Aphelidea (Tedersoo *et al.*, 2018); or the opposite, with Aphelidea as sister to the true Fungi and the two together sister to Rozellida + Microsporidia (Torruella *et al.*, 2018).

(*a*) *Microsporidia*

Microsporidia is a diverse group of intracellular obligate parasites of metazoans and occasionally gregarines (Metchnikovellidae). Microsporidian parasites of insects and vertebrates have been widely studied, with dozen of fully sequenced genomes available. However, microsporidians outside this range of hosts are poorly described, and some environmental studies suggest that they must present a large, undescribed diversity based on their host range and endemicity (Ardila-Garcia *et al.*, 2013). As a result of their lifestyle, they present very reduced genomes, to the point that they have some characteristics typical of prokaryotic genomes, such as overlapping genes (Peyretaillade *et al.*, 2011). They also lack motile structures and, with the exception (so far) of *Mitosporidium daphniae*, true mitochondria (Haag *et al.*, 2014), possessing instead mitochondria-derived organelles called mitosomes. Mitosomes lack a genome, and their main function seems to be the assembly of iron–sulfur clusters (Stairs, Leger, & Roger, 2015). Many members of this clade have lost the ability to perform glycolysis and the tricarboxylic acid cycle, relying on scavenging ATP directly from the host cell *via* an array of horizontally acquired genes (Cuomo *et al.*, 2012; Alexander *et al.*, 2016). They present a highly specialized harpoon-like penetration structure termed the polar tube that is a highly modified Golgi apparatus (Xu & Weiss, 2005; Beznoussenko *et al.*, 2007). Simplified cellular morphology, lack of mitochondria and long-branch-attraction phylogenetic artefacts caused by their parasitic nature, led to the hypothesis that Microsporidia were early-branching eukaryotes, whose divergence preceded the acquisition of mitochondria (Corradi & Keeling, 2009). Later on, the description of mitosomes and several mitochondria-related genes in their genomes refuted such hypothesis, and further phylogenetic studies pointed at a close relatedness to fungi, either as a highly derived fungal clade or as a sister group to the rest of the kingdom. Phylogenomic analyses favoured the latter hypothesis, joining *Rozella allomycis* as sister to all other fungi (Capella-Gutiérrez, Marcet-Houben, & Gabaldón, 2012; James *et al.*, 2013). This prompted the official adoption of Microsporidia by mycologists (McNeill *et al.*, 2012). Yet the nomenclatural rules for this group still follow protist conventions instead of classical botanical rules applied to other fungi. May this legacy remind us of the taxonomic rollercoaster they have gone through.

(*b*) *Rozellidea*

Rozella is a genus of flagellated parasitoids of zoosporic fungi (Chytridiomycota and Blastocladiomycota), Oomycetes, and some green algae (Gleason *et al.*, 2012). *Rozella* presents a zoosporic infectious stage that attaches to the host cell. After this, the protoplasm of *Rozella* invades the host until it has occupied all available space. At this point, the parasite sporulates, completing the life cycle (Foust, 1937; Letcher *et al.*, 2017, 2018; Powell, Letcher, & James, 2017). Some species can form resting spores, sometimes presenting spines. The genome of *Rozella allomycis*, a parasitoid of the blastoclad *Allomyces* was published in 2013 (James *et al.*, 2013). Unlike most Microsporidia, *Rozella* presents a non-reduced genome and true mitochondria (James *et al.*, 2013), although with reduced mitochondrial metabolism. Rozellidea also includes the recently described *Paramicrosporidium* and *Nucleophaga*,

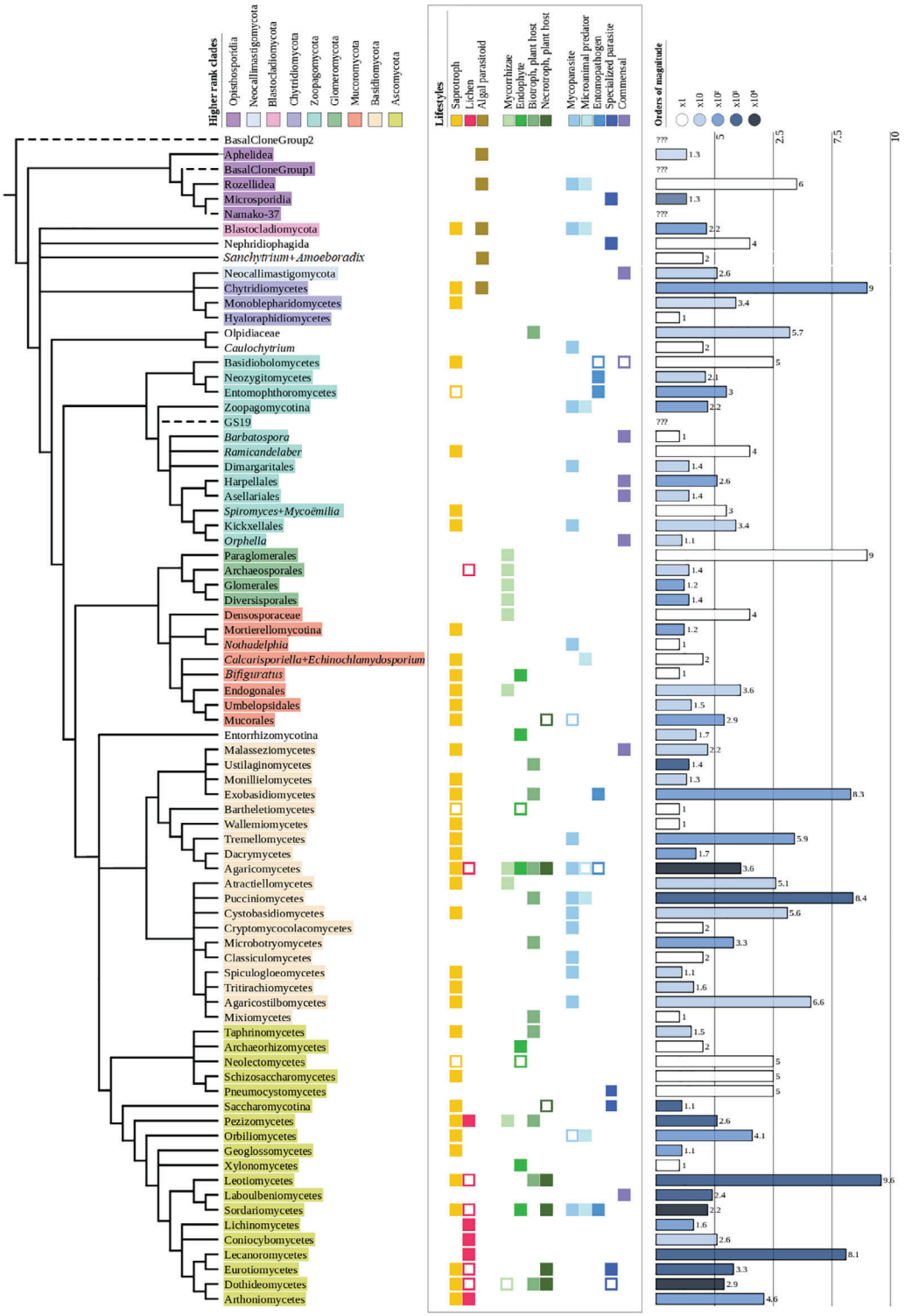

Fig. 1. The fungal tree of life. Tree showcasing currently described groups within the Kingdom Fungi up to the class level, as well as *incertae sedis* lineages that cannot be assigned to any other class. In the case of zygomycetous fungi, due to historical reasons, we have included lineages up to order level. The first column uses colours to cluster clades in corresponding phyla. The second column compiles the lifestyles present in each group. Empty squares indicate that the given lifestyle is anecdotic or hypothetical. The third column shows the number of described species in each group according to the Catalogue of Life (Bisby & Roskov, 2010) or, for certain groups that are not represented in this database, Wikispecies (Wikimedia, 2011). Since the number of species might vary by several orders of magnitude, species number bars are coded using different colours. Tree generated using the interactive Tree of Life (iTOL) server (Letunic & Bork, 2016).

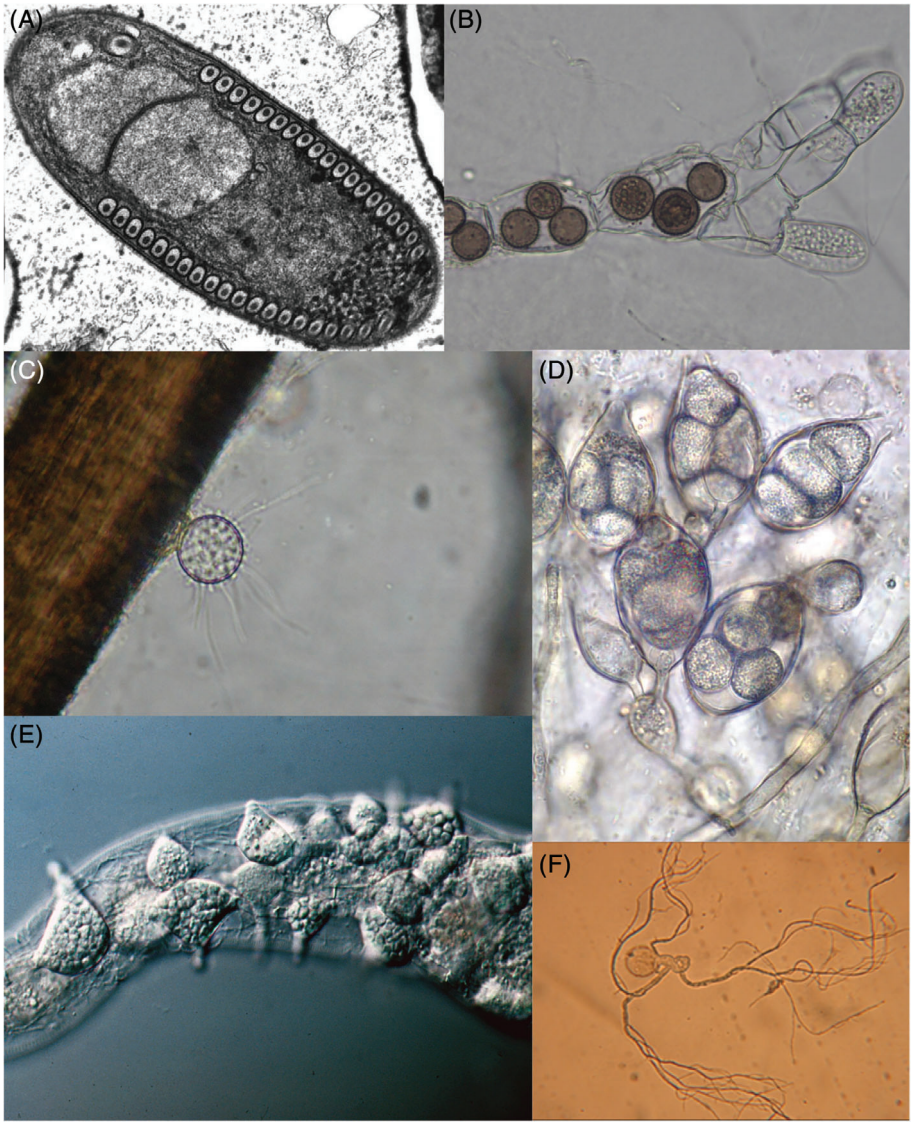

Fig. 2. Diversity of zoosporic Fungi. (A) Transmission electron micrograph of a sporoblast of *Fibrillanosema crangonycis* (Microsporidia). The nucleus is clearly visible in the image and a series of concentrical structures with a highly electrodense core that appear tightly packed around the perimeter of the cell. This peculiar structure corresponds to a coiled polar tube, an infective harpoon-like structure characteristic of Microsporidia. Original photograph taken by Leon White, CC BY-SA 3.0 license. (B) Mature zoosporangia of *Rozella allomycis* (Rozellidea) during the last stages of infection of a mycelium of *Allomyces* sp. (Blastocladiomycota). Like many zoosporic fungi, *Rozella* is a parasitoid that invades and consumes the host cytoplasm, after which it produces sporangia. Original photograph by Timothy Y. James, CC BY-SA 3.0 license. (C) Zoosporangium of *Rhizophidium keratinophylum* (Chytridiomycetes), appearing as a globular structure, growing on a human hair (fibrous brown structure). Beyond their parasitic roles, many chytrids have important roles in aquatic environments as saprotrophs specialized for degrading highly recalcitrant organic matter, such as pollen grains, arthropod exuviae or keratin. Original photograph by Wikipedia user TelosCricket, CC BY-SA 4.0 license. (D) Micrograph of a group of oogonia from *Gonapodya polymorpha* (Monoblepharidomycetes, Chytridiomycota). The Monoblepharidomycetes are the only group of Fungi that present morphologically distinct gametes (i.e. anisogamy). They are also the only group within Chytridiomycota that have developed true hyphae, which evolved independently from those of terrestrial Fungi. Original photograph by Marilyn R. N. Mollicone. All rights reserved. (E) Mature sporangia of *Catenaria anguillulae* (Blastocladiomycota) growing inside a nematode alongside a true mycelium. Despite its relatively low number of species, Blastocladiomycota is a highly diverse group in terms of ecology, including saprotrophs, plant pathogens, algal parasitoids and even animal parasites. *Catenaria*, in particular, has been studied for its potential use as a pest-control agent in agriculture. Original photograph by George Barron. Licensed for non-commercial academic and research use only. (F) Microscopic preparation of a monocentric thallus from *Neocallimastix frontalis* (Neocallimastigomycota) isolated from deer faeces. The thallus possess a bulbous structure that corresponds with the zoosporangia and a series of root-like protrusions, the rhizoids. The Neocallimastigomycota are a group of Fungi almost exclusively associated with the gut of herbivorous mammals. They have lost their mitochondria and present a highly expanded repertoire of cellulolytic enzymes. Original photograph from Atanasova-Pancevska & Kungulovski (2017), CC BY-NC 4.0 license.

Table 1. Main lineages within Opisthosporidia and the zoosporic fungi. Due to changes in the scope of certain historical clades, references might not refer to the initial published description but rather to more recent bibliography

Name and references	Main described lifestyles	Main traits	Representative genera
Opisthosporidia (Karpov *et al.*, 2014*a*)	Intracellular parasites and parasitoids	Many are zoosporic or amoeboid; lacking chitin-based cell wall, although chitin might be present in resting stages	
Aphelida (Gromov, 2000; Adl *et al.*, 2012)	Parasitoids of photosynthetic unicellular eukaryotes	Intracellular unwalled stage as a phagotrophic amoeba; characteristic food vacuole with excretory body; ciliated or amoeboid dispersal cells; tubular or lamellar cristae	*Aphelidium*, *Amoebaphelidium*
Rozellida (Lara *et al.*, 2010; Jones *et al.*, 2011) syn. Cryptomycota, Rozellomycota	Parasitoids of diverse organisms	Zoosporic; intracellular unwalled stage with digitiform protrusions, may be phagotrophic	*Rozella*, *Nucleophaga*
Microsporidia (Adl *et al.*, 2012)	Intracellular parasites of metazoans	Mitochondria reduced to mitosome; polar tube	*Nosema*, *Spraguea*, *Encephalitozoon*, *Amphiamblys*, *Metchnikovella*
Chytridiomycota (Hibbett *et al.*, 2007)	Free-living saprobes and parasitoids	Zoosporic, uniflagellated, sometimes as crawling cells; rhizoid formation; stacked Golgi apparatus	
Chytridiomycetes (Hibbett *et al.*, 2007)	Free-living saprobes and parasitoids	Thallus monocentric or rhizomycelial polycentric	*Spizellomyces*, *Chytridium*, *Batrachochytrium*, *Homoloaphlyctis*, *Rhizophlyctis*, *Arkaya*, *Kappamyces*
Hyaloraphidiomycetes (Ustinova *et al.*, 2000)	Unknown	Lack of flagellum or rhizoid; crescent-shaped cells; reproduction by 4–8 spores within cells that present the same structure as the mother cell; stacked Golgi dictyosomes	*Hyaloraphidium*
Monoblepharidomycetes (Adl *et al.*, 2012; Tedersoo *et al.*, 2018) syn. Neocallimastigomycotina	Free-living saprobes and parasitoids	Thallus filamentous, sometimes forming true hyphae or unbranched; two centrosomes in parallel; flagellum unique steming from one centrosome; second centrosome is striated with radiating microtubules; oogamy	*Gonapodya*, *Monoblepharis*, *Oedogoniomyces*
Neocallimastigomycota (Hibbett *et al.*, 2007) syn. Neocallimastigomycotina, Neocallimastigomycetes within Chytridiomycota	Associated with the gut of mammals and some reptiles; anaerobic cellulose decomposer	Zoosporic, sometimes with many flagella; mitochondria reduced to hydrogenosomes; extremely low %GC; highly developed carbohydrate metabolism	*Neocallimastix*, *Piromyces*, *Orpinomyces*
Blastocladiomycota (James *et al.*, 2006*b*)	Saprobes; animal parasites, algal parasitoids, plant pathogens	Zoosporic, uniflagellated; cone-shaped nucleus with particular kinetocore ultrastructure; some species produce true hyphae	*Allomyces*, *Catenaria*, *Blastocladia*, *Physoderma*

which are microsporidian-like parasites of amoebozoa (Corsaro *et al.*, 2014*a*,*b*, 2016). It is noteworthy that the trophobiont stages of *Nucleophaga* and *Rozella* are covered by digitiform protrusions (Powell, 1984; Corsaro *et al.*, 2014*a*, 2016), suggesting some form of phagocytic capabilities. Environmental sequences phylogenetically related to *Rozella* have been found in virtually all aquatic environments, comprising a very high sequence divergence. Such distribution and divergence was interpreted as the existence of a highly species-rich and ecologically meaningful hidden clade, which could be comparable in diversity to the rest of true fungi (Corsaro *et al.*, 2016). However, given the known characteristics of *Nucleophaga* and *Paramicrosporidium*, such conclusions may be premature. If we extrapolate our knowledge of Microsporidia to these microsporidian-like organisms, it is plausible to assume that high evolutionary rates may inflate estimations of real taxonomic diversity, leading to incorrect interpretations of large sequence divergence as evidence of diversity at high taxonomical rank.

(*c*) *Evolutionary relationships between Microsporidia and Rozellidea*

The relationship between Microsporidia and Rozellidea and the existence of both groups as independent phylogenetic lineages is currently the subject of debate (Corsaro *et al.*, 2016; Torruella *et al.*, 2018). While *Rozella* has several

morphological traits that set it apart from Microsporidia, the same cannot be said about *Paramicrosporidium* and *Nucleophaga*. Similarities between the two groups run deeper than morphology. Several important metabolic characteristics such as the horizontally acquired strategies for nucleoside scavenging from the host, or loss of amino acid biosynthetic pathways and mitochondrial electron transport chain are found in both Rozellidea and Microsporidia (Quandt *et al.*, 2017). However, the distribution of several of these traits is rather patchy, implying parallel reductive evolution. *Mitosporidium*, a parasite of the water flea *Daphnia pulex*, has been placed closer to *Rozella* than to the core Microsporidia (Corsaro *et al.*, 2016). The partial sequence of the metchnikovellidan *Amphiamblys* suggests a phylogenetic position even further away from the core of Microsporidia than *Mitosporidium*, which would probably imply affinity with Rozellidea (Corsaro *et al.*, 2016). Phylogenomic analyses of *Paramicrosporidium* recover it as a sister to core Microsporidia + *Mitosporidium* (Mikhailov, Simdyanov, & Aleoshin, 2017). Genomic analyses of *Metchnikovella incurvata* confirm Metchnikovellidae as a distinct and early branching clade within Microsporidia (Galindo *et al.*, 2018). No phylogeny including both Rozellidea and any member of the Metchnikovellidae has been published to date. Evaluation and description of additional microsporidian-like parasites of hosts outside insects and vertebrates are likely to blur the line between Rozellidea and Microsporidia even further. This situaton has led to some authors expanding the definition of Microsporidia to include *Paramicrosporidium* and *Nucleophaga*, leaving Microsporidia and *Rozella* as two separate monophyletic clades (Quandt *et al.*, 2017; Bass *et al.*, 2018).

(*d*) *Aphelidea*

The last major lineage to join the fungal family are the Aphelidea. Only four genera have been described in this group to date: *Aphelidium*, *Amoebaphelidium*, *Paraphelidium* and *Pseudaphelidium* (Karpov *et al.*, 2017*b*). Their life cycle consists of a motile cell that is either flagellated (*Aphelidium*, *Pseudaphelidium*), amoeboid (*Amoebaphelidium*) or both (*Paraphelidium*). Occasionally, the zoospore may form a cyst, which can act either as a resistance form or as part of the penetration mechanism (*Paraphelidium*). Once inside the host, the parasitoid develops as a multinucleated plasmodium. The plasmodium divides into uninucleated zoospores after it has consumed the host cytoplasm by phagocytosis and releases the zoospores through the penetration site (Karpov *et al.*, 2014*b*, 2017*b*). Despite having just a few formally described species, environmental sampling suggests that Aphellidea is indeed a highly diverse and cosmopolitan clade (Karpov *et al.*, 2014*b*). It remains unknown whether deviations to the described life cycle exist in nature.

(2) **Chytridiomycota**

Chytridiomycota are divided into three main classes: Chytridiomycetes, Monoblepharidomycetes and Hyaloraphidiomycetes (James *et al.*, 2006*a*; Sekimoto *et al.*, 2011). Chytrids present a zoosporic disemination stage and usually a growing non-flagellated stage. Chytrid cells can present different degrees of apical growth, such as filopodia and rhizoids, but in such cases the cell has a single nucleus and the protrusions are not cylindrical. Despite the presence of filopodia in several chytrid groups (e.g. *Batrachochytrium*) (Fritz-Laylin, Lord, & Mullins, 2017), true phagocytosis has never been described. Multinucleated non-cylindrical growth forms, known as rhizomycelia, have been observed in several clades. True mycelial growth is restricted to certain genera within the Monoblepharidomycetes (Dee *et al.*, 2015). Chytrids are important pathogens of plants (e.g. *Synchitrium*), animals (e.g. *Batrachochytrium*), parasites of several groups of algae (e.g. *Chytridium*, *Dinomyces*), as well as decomposers of highly recalcitrant organic matter, such as pollen (e.g. *Spizellomyces*, *Rhyzophidium*), cellulose (e.g. *Rhizophlyctis*), arthropod exoskeletons, and fungal spores. Parasitic chytrids seem to play a key role in aquatic environments, controlling algal biomass and blooms, recycling nutrients, and acting as food for small animals in a nutrient loop that has been termed the 'mycoloop' (Gleason, Schmidt, & Marano, 2010; Rasconi, Niquil, & Sime-Ngando, 2012; Kagami, Miki, & Takimoto, 2014; Frenken *et al.*, 2016, 2017). The mycoloop is not restricted to members of the Chytridiomycota *sensu stricto*, as involvement of other zoosporic fungi such as members of the Aphelidea and Rozellidea is known (Gleason *et al.*, 2012, 2014; Ishida *et al.*, 2015). In land environments their presence is usually minor, although they form the main component of the fungal fraction in certain soil environments, such as periglaciar soils (Freeman *et al.*, 2009). Environmental studies have found a myriad of putative novel clades within the phylum or as phylum-level lineages closely related to chytrids, particularly in marine and soil environments (Nagahama *et al.*, 2011; Manohar *et al.*, 2013; Richards *et al.*, 2015; Tedersoo *et al.*, 2017). Sequence information on zoosporic fungi is currently very limited, which poses challenges to obtaining a robust chytrid tree of life. This situation fortunately is changing, and thanks to the application of single-cell-based techniques genomic and environmental sampling is steadily increasing (Grossart *et al.*, 2016; Ahrendt *et al.*, 2018).

(*a*) *Chytridiomycetes*

Chytridiomycetes is by far the largest class of zoosporic fungi with around 1000 described species. Based on phylogenetic analyses and the ultrastructure of the zoosporic stage, several lineages have been raised to the level of orders. The phylogenetic affinity of several genera, as well as the relationships of the different orders within the class is still not fully resolved (Misra, Tewari, & Deshmukh, 2012; Powell & Letcher, 2014). The picture will become further complicated as new environmental chytrids are described. Chytridiomycetes have received considerable attention in recent years owing to *Batrachochytrium dendrobatidis*, a parasite that is devastating populations of amphibians worldwide (Longcore, Pessier, & Nichols, 1999; Berger *et al.*, 2005). The genome of *Batrachochytrium dendrobatidis*, published in 2009, represented the first sequenced chytrid (Cuomo & Birren, 2010).

(*b*) *Monoblepharidomycetes*

Monoblepharidomycetes comprise a group of freshwater, zoosporic fungi that can present either unicellular or mycelial growth. The mycelial Monoblepharidomycetes (*Gonapodya*, *Monoblepharys* and *Monoblepharella*) form a monophyletic clade within the class (James *et al.*, 2006*a*; Sekimoto *et al.*, 2011). They are the only described chytrids that form true hyphae, which in turn present some unique cytological characteristics, such as the presence of centrioles and the absence of Spitzenkörper, which point to an independent origin of these traits from the other fungi (Sekimoto *et al.*, 2011; Dee *et al.*, 2015). An oogonic sexual cycle (i.e. the presence of morphologically different gametes) is common in Monoblepharidomycetes, a unique feature among fungi. *Hyaloraphidium* is a poorly studied organism with an unclear lifestyle that was classified originally as a colourless green algae (Ustinova, Krienitz, & Huss, 2000), but molecular phylogenies show affinity with Monoblepharidomycetes (Forget *et al.*, 2002; Sekimoto *et al.*, 2011). As such, it has been classified as either a member of the Monoblepharidomycetes or as its own class, Hyaloraphidiomycetes (Schoch *et al.*, 2014; Tedersoo *et al.*, 2018). It is important to note that this lineage has lost its flagellum independently from the main terrestrial fungi (Ustinova *et al.*, 2000; James *et al.*, 2006*b*).

(3) Neocallimastigomycota

Neocallimastigomycota comprises a small group of flagellated, obligate anaerobic, non-parasitic fungi. The group is formed by a single family currently comprising 18 recognized genera (Powell & Letcher, 2014; Hanafy *et al.*, 2017; Wang, Liu, & Groenewald, 2017; Hanafy, Elshahed, & Youssef, 2018; Joshi *et al.*, 2018; Hanafy *et al.*, 2019), of which some may be paraphyletic (Wang *et al.*, 2017). They lack true mitochondria, harbouring mitochondria-derived hydrogenosomes instead. Some genera are multiflagellated. The nuclear envelope remains intact during mitosis. As a result of adaptation to anaerobic environments, members of this group do not synthesize ergosterol, whose biosynthetic pathway requires oxygen, but use tetrahymenol instead (Weete, Abril, & Blackwell, 2010). Similarly to Chytridiomycota, pluricellular forms seem to lack true hyphal organization. Neocallimastigomycota present large genomes (101 Mb in *Orpinomyces*) with high content of repetitive elements and a very low GC content (as low as 17% in *Orpinomyces*) (Billon-Grand *et al.*, 1991; Youssef *et al.*, 2013). These genomes harbour a very wide and rich repertoire of carbohydrate-degrading enzymes (Youssef *et al.*, 2013; Gruninger *et al.*, 2014), shaped by gene expansions and horizontal gene-transfer events (Garcia-Vallvé, Romeu, & Palau, 2000; Murphy *et al.*, 2019; Wang *et al.*, 2019). Members of this phylum have been isolated or detected almost exclusively in the gut of herbivorous mammals and iguanas, where they decompose plant organic matter. Outside this environment, there is a single report of the presence of these fungi in the gut of a sea urchin, based on morphological identification (Thorsen, 1999), indicating the potential of yet to be sampled diversity within the group. Unlike most fungal lineages, members of this phylum have rather high optimal growth temperatures as a consequence of their animal-associated lifestyle.

The phylogenetic position of Neocallimastigomycota remains elusive, and thus its status as a phylum is debated. Some studies place them as the sister branch to Chytridiomycota *sensu stricto* (James *et al.*, 2006*a*,*b*; Ebersberger *et al.*, 2012; Bauer *et al.*, 2015), while other phylogenetic analyses place Neocallimastigomycota within Chytridiomycota *sensu stricto*, with Monoblepharidomycetes as sister to the rest of Chytridiomycota + Neocallimastigomycota (Sekimoto *et al.*, 2011) (Fig. 3). Molecular dating suggests that the group is rather modern, having diversified in association with the emergence of grasses (Poaceae) and herbivorous mammals (Wang *et al.*, 2019). This recent origin might suggest that the Neocallimastigomycota are in fact a highly specialized lineage that has emerged from within another zoosporic lineage, but the specifics of this presumed affinity are still unresolved.

(4) Blastocladiomycota

The phylum Blastocadiomycota comprises a relatively small group of zoosporic fungi with diverse morphological and ecological traits. Before its promotion to a phylum level based on molecular phylogenetic studies (James *et al.*, 2006*b*), the group was already recognized as monophyletic based on ultrastructural similarities (Cavalier-Smith, 1981), uniting them with terrestrial fungi. Unlike other zoosporic fungi, Blastocladiomycota present alternation of gametophytic and sporophytic generations. They present up to three types of uniflagellated zoospores, asexual meiospores and sexual gametes. Sexual reproduction is not known in all groups. True mycelial growth (sometimes presenting pseudosepta) is recognized, while amoeboid crawling stages have not been described. The zoospores present a characteristic nuclear cap that, in hyphal species, produces bipolar growth. The resting sporangium is typically darkly pigmented and usually presents spines and other ornamentations (James, Porter, & Martin, 2014). In other respects, Blastocladiomycota are very similar in their ecological and general morphological characteristics to members of the Chytridiomycota *sensu stricto*, with species that are saprobes in soils and freshwater environments, invertebrate parasites, and plant and algal pathogens (Porter *et al.*, 2011; James *et al.*, 2014). The group contains two formerly popular model organisms, *Allomyces macrogynus* and *Blastocladiella emersonii*, which are two saprotophs with well-defined and well-studied alternation of generations. The genus *Coelomomyces* grows as unwalled tubular thalli in an insect or crustacean host, a cellular organization that has been compared to that observed in members of the Entomophthoromycotina (Gleason *et al.*, 2010).

Historically associated with the other zoosporic fungi, molecular studies initially showed great divergence from them (Bowman *et al.*, 1992; Bruns *et al.*, 1992; James *et al.*, 2000; Lutzoni *et al.*, 2004). Blastocladiomycota were dragged into controversies regarding the paraphyly of Zygomycota, appearing as the sister branch to Entomophthoromycotina

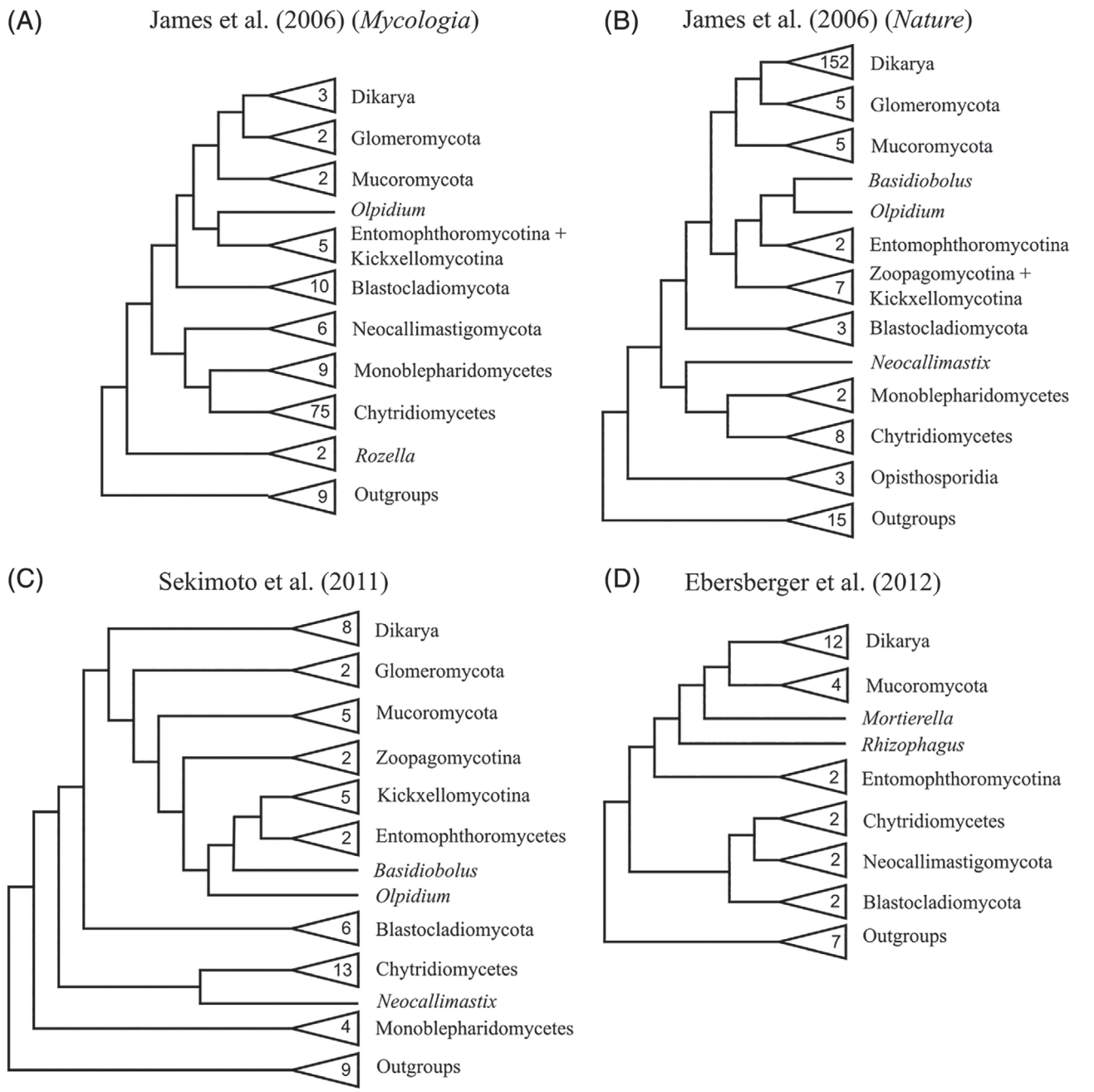

Fig. 3. Phylogenetic position of Neocallimastigomycota in different studies. Simplified topology from several phylogenetic studies covering the phylogenetic position of Neocallimastigomycota. Numbers inside triangles represent the number of sampled species within the clade. (A) Topology obtained from James *et al.* (2006*b*). Phylogeny constructed from a concatenation of 18S rRNA, 28S rRNA and 5.8S rRNA, using Bayesian inference. (B) Topology obtained from James *et al.* (2006*a*). Phylogeny constructed from a concatenation of 18S rRNA, 28S rRNA, 5.8S rRNA, EF1-α, RPB1 and RPB2, using Bayesian inference. (C) Topology obtained from Sekimoto *et al.* (2011). Phylogeny constructed from RPB1, RPB2, EF1-α, rRNA and actin genes, using a maximum-likelihood approach. (D) Topology obtained from Ebersberger *et al.* (2012). Phylogeny reconstructed from a supermatrix of 46 single-copy genes, using a maximum-likelihood approach.

in some studies (Tanabe *et al.*, 2005; Tretter *et al.*, 2013). This placement was shown to be caused by high evolutionary rates in certain genera in the Zoopagomycota. Correction of these artefacts and the availability of additional sequences for molecular analyses led to the recovery in most phylogenetic studies, albeit with low support, of Blastocladiomycota as the sister branch to all terrestrial fungi + *Olpidium* (Sekimoto *et al.*, 2011; Ebersberger *et al.*, 2012; Torruella *et al.*, 2012; Spatafora *et al.*, 2016; Tedersoo *et al.*, 2018). The phylum contains a single order, Blastocladiales, and

five morphologically defined families that were validated with minor changes by molecular studies (Porter *et al.*, 2011; James *et al.*, 2014). Environmental sampling has detected Blastocladiomycota clades at high abundances in aquatic environments, both marine and fresh water (Tedersoo *et al.*, 2017). Some studies suggest that they might be prevalent in oxygen-poor environments (James *et al.*, 2014).

III. ZYGOMYCETOUS FUNGI

Loss of their flagellar apparatus and the development of hyphal growth allowed a particular group of Fungi to conquer emerged lands. These terrestrial Fungi include most described diversity, included in the subkingdom Dikarya (Basidiomycota + Ascomycota + Entorrhizomycota) plus several lineages collectively called zygomycetous Fungi. 'Zygomycetous' refers to a paraphyletic phylum (Zygomycota), and this in turn to a sexual structure, the zygospore, that is common to most lineages ascribed to it. We include here the Glomeromycota, despite their historical separation from the 'Zygomycota' due to the absence of observed zygospores (or any sexual structure), for the sake of simplicity and in light of recent taxonomic revisions that advocate the incorporation of Glomeromycota into the Mucoromycota. With this in mind, zygomycetous Fungi form two main lineages, one that is composed mostly of parasites of opisthokonts (Zoopagomycota; see Table 2) and a second that is composed mostly of plant symbionts and saprotrophs (Glomeromycota + Mucoromycota; see Table 3). Figure 4 illustrates some of these organisms.

(1) Zoopagomycota

This phylum is the earliest diverging group of non-flagellated fungi, and includes three main lineages: Zoopagomycotina, Entomophthoromycotina and Kickxellomycotina (Hibbett *et al.*, 2007; Spatafora *et al.*, 2016). These three lineages have the ability to form true mycelia. Most members are either saprotophs or parasites of metazoans, amoebae or other fungi, including highly specialized forms. Virtually no morphological characteristics unite the three subphyla, which are classified together based on phylogenetic affinity and their general metazoan-associated lifestyle.

(a) *Entomophthoromycotina*

Entomophthoromycotina comprises three main classes: Basidiobolomycetes, Neozygitomycetes and Entomophthoromycetes (Humber, 2012). All groups in the Entomophthoromycotina present 24-methyl cholesterol as their main membrane sterol (Weete *et al.*, 2010). Basidiobolomycetes is the earliest-splitting lineage and comprises the genus *Basidiobolus*, a saprotrophic gut commensal of amphibians and reptiles and opportunistic human pathogen (Manning, Waters, & Callaghan, 2007; Manning & Callaghan, 2008), and the yeast-like snake pathogen *Schizangiella* (Gryganskyi *et al.*, 2013; Benny, Humber, & Voigt, 2014). *Basidiobolus* is so far the only genus in the Entomophthoromycotina to present septate hyphae. *Basidiobolus* and *Conidiobolus* are unique among the zygomycetous fungi for possessing a true Spitzenkörper (Roberson *et al.*, 2011; Fisher *et al.*, 2018). The second class, Neozygitomycetes, comprises several genera of parasites of mites and aphids. Unfortunately, very little sequencing data are available for this group, raising doubts about its taxonomic uniqueness, its phylogenetic placement and even its membership in this subphylum (White *et al.*, 2006; Gryganskyi *et al.*, 2013).

The Entomophthoromycetes is the most species-rich and best-characterized class in the subphylum. It comprises mainly the genus *Conidiobolus* (family Ancylistaceae) (a saprobe, facultative insect parasite and occasional human pathogen), several families of mostly specialized insect parasites that form a well-defined monophyletic group, and some small genera with diverse ecological strategies: *Ancylistes* (Ancylistaceae) is a parasite of desmid algae, *Macrobiotophthora* (Ancylistaceae) parasitises nematodes and tardigrades, *Completoria* (Completoriaceae) is a fern biotrophic parasite, and *Meristacrum* (Meristacraceae) is a nematode parasite (Gryganskyi *et al.*, 2012, 2013; Humber, 2012). Nuclear characters (size, presence, stainability, nucleolar characteristics and pattern of mitosis) and modes of germination of resting spores are important for their systematics at a family level (Humber, 1989; Benny *et al.*, 2014). The available genetic information on these lineages is very limited, and thus their taxonomy might be revised in the near future (Gryganskyi *et al.*, 2013; Benny *et al.*, 2014). The family Ancylistaceae was the earliest to split within the Entomophthoromycetes, although sequencing data are mostly limited to *Conidiobolus* species and phylogenetic analyses have typically failed to recover monophyly of this genus (Gryganskyi *et al.*, 2013; Spatafora *et al.*, 2016). Another common ecological strategy is found in a monophyletic group of highly specialized entomopathogenic fungi comprising around 200 species (*Entomophthora*, *Massospora*, *Pandora*, *Entomophaga*). These parasites usually grow as unwalled mycelia within the host's coelomatic cavity, where they commonly reach considerable biomass before killing the host. This intimate association with the host for most members of the Entomophthoromycotina has made the collection of samples for DNA-based analyses challenging, but morphological studies have proved to be generally consistent with molecular phylogenies (Humber, 2012; Gryganskyi *et al.*, 2013).

(b) *Zoopagomycotina*

Zoopagomycotina comprises a single order, Zoopagales, that includes five families and around 20 genera (Hibbett *et al.*, 2007; Benny *et al.*, 2014, 2016; Degawa, 2014). The genus *Basidiolum* is suspected to belong to this subphylum (Benny *et al.*, 2016). They live as parasites of free-living amoebae (Zoopagaceae, Cochlonemataceae), soil microinvertebrates (Helicocephalidaceae, Zoopagaceae and Cochlonemataceae) or other fungi (Piptocephalidaceae and

Table 2. Main lineages within Zoopagomycota. Due to changes in the scope of certain historical clades, references might not refer to the initial published description but to more recent bibliography. For historical reasons we have decided to keep the ordinal assignation within zygomycetous fungi, although we consider that these clades are likely to be elevated to a higher taxonomic rank as proposed by several authors

Name	Main described lifestyles	Main traits	Representative genera
Zoopagomycota (Spatafora *et al.*, 2016; Tedersoo *et al.*, 2018)	Saprobes, invertebrate parasites, mycoparasites, amoebophagous	Thallus mycelial, mostly separated into cells with complete or uniperforate septa; sexual reproduction, if present, *via* zygospores by gametangial conjugation	
Zoopagomycotina (Hibbett *et al.*, 2007)	Parasites of small invertebrates, amoebae and fungi	Very small thallus, generally coenocytic; uniperforated septa appear in certain nematode-trapping genera; sexual reproduction with globose zygospores	*Zoopage*, *Piptocephalis*, *Rhopalomyces*, *Amoebophylus*
Entomophthoromycotina (Hibbett *et al.*, 2007)	Insect parasites; occasionally saprobes or plant parasites	Coenocytic hyphae, yeast or unwalled syncitia growing within the host	
Basidiobolomycetes (Humber, 2012)	Saprotrophs and facultative insect parasites; sometimes associated with reptiles and amphibians	Hyphal or yeast-like; large nucleus with large central nucleolus; zygospores with thick bi-layered cell walls; globose conidia, released by a rocket-like mechanism	*Basidiobolus*, *Schizangiella*
Entomophthoromycetes (Hibbett *et al.*, 2007)	Obligate insect parasites; *Conidiobolus* lives as a saprotroph and facultative insect parasite	Filamentous without septa; grow as an unwalled syncitia within host; ballistic conidia; 24-methyl cholesterol as main membrane sterol	*Entomophthora*, *Pandora*, *Massospora*, *Conidiobolus*
Neozygitomycetes (Humber, 2012)	Parasites of hemipterans and orthopterans	Melanized spores; vermiform, moderately sized chromosomes that condense during mitosis on a central metaphase plate but uncoil during interphase; nuclear numbers in vegetative cells and conidia are low and apparently controlled at 3–5	*Neozygites*, *Thaxterosporium*
Kickxellomycotina (Hibbett *et al.*, 2007)	Parasites or symbionts of arthropods, mycoparasites, saprobes	Presence of septa with plugs, morphology diagnostic of the different clades; mycelium regularly septated	
Asellariales (Hibbett *et al.*, 2007)	Associated with the gut of isopods and springtails	Filamentous, branched thalli; asexual reproduction by arthrospore-like cells that disarticulate; lenticular septa	*Asellaria*, *Baltomyces*, *Orchesellaria*
Dimargaritales (Hibbett *et al.*, 2007)	Haustorial mycoparasites, mostly on Mucoromycotina	Thallus branched, with septate hyphae, producing septate sporangiophores; septa with median disciform cavities containing biconvex plugs with polar protuberances; asexual reproduction by bisporous merosporangia	*Dimargaris*, *Dispira*, *Tieghemiomyces*
Harpellales (Hibbett *et al.*, 2007)	Associated with the gut of aquatic insects	Basal cell attached to the host from which a filamentous septate thallus emerges; septa with lenticular plugs; asexual reproduction by lateral elongate monosporous trichospores; sexual reproduction by conical or biconical zygospores	*Harpella*, *Smittium*
Kickxellales (Hibbett *et al.*, 2007)	Saprobes or mycoparasites	Thallus branched, with septate hyphae; septa with median disciform cavities containing biconvex plugs; asexual reproduction by monospored sporangiola on sporocladia; sexual reproduction by nearly globose zygospores	*Coemansia*, *Kickxella*, *Martensiomyces*, *Ramicandelaber*
Ramicandelaber (Tedersoo *et al.*, 2018)	Saprobe	Sporangiophores septate, verticillately branched, forming supporting septated hyphae with rhizoids; branches cylindrical or ellipsoid, with further irregular branching	*Ramicandelaber*
Barbatospora (Tretter *et al.*, 2014)	Associated with aquatic larvae of Simuliidae	Branched septate thallus with basal cell; cap-like structure at the end of the trichospores, which falls away at maturity to reveal a set of appendage-like structures; unknown zygospores and septal morphology	*Barbatospora*
Orphella (Tretter *et al.*, 2014)	Associated with aquatic larvae and nymphs of Plecoptera	Coiled asexual spores and zygospores; basal cell attached to the host from which a filamentous branched septate thallus emerges; unknown septal morphology	*Orphella*
Spiromyces + *Mycöemilia* clade (Kurihara, Degawa, & Tokumasu, 2004; Tedersoo *et al.*, 2018)	Saprobes, isolated from dung and soil	Septate hyphae; lenticular septal plug; sporophores erect, septate, branched or unbranched, producing one to several fertile parts	*Spiromyces*, *Mycöemilia*

Table 3. Main lineages within Mucoromycota and Glomeromycota. Due to changes in the scope of certain historical clades, references might not refer to the initial published description but to more recent bibliography. For historical reasons we have decided to keep the ordinal assignation within zygomycetous fungi, although we consider that these cladess are likely to be elevated to a higher taxonomic rank as proposed by several authors

Name	Main described lifestyles	Main traits	Representative genera
Mucoromycota (Adl *et al.*, 2012; Spatafora *et al.*, 2016)	Mostly filamentous saprobes; occasionally mycoparasites, plant pathogens or mycorrhizal	Coenocytic hyphae, able to perform anastomosis; mature hyphae sometimes irregularly septated; rhizoids common	
Mortierellomycotina (Hoffmann *et al.*, 2011)	Filamentous saprobes	Absence of columella; dichotomous branching	*Mortierella*, *Aquamortierella*, *Dissophora*
Mucoromycotina (Hibbett *et al.*, 2007)	Filamentous saprobes; occasional mycoparasites, plant pathogens or ectomycorrhizal	Chitosan as main structural polysaccharide; sporangia with well-developed columella	
Endogonales (Hibbett *et al.*, 2007; Adl *et al.*, 2012)	Ectomycorrhizal and saprobe	Zygospores with apposed suspensors in a subterranean sporocarp	*Endogone*
Umbelopsidales (Spatafora *et al.*, 2016)	Saprobes	Thallus branched; hyphae initially without septa but developing near the branch point; asexual reproduction *via* sporangia; sporangiophores densely branched, with septa distant from the sporangium; sporangia reddish or ochraceous, globose or elongate, multispored or single-spored; columella usually conspicuous; chlamydospores abundant, filled with lipids in culture; unknown sexual stages	*Umbelopsis*
Mucorales (Adl *et al.*, 2012)	Saprobes, ocasionally mycoparasites or plant pathogens	Filamentous, septa absent except in older hyphae; plasmodesmata at septal pores	*Mucor*, *Phycomyces*, *Saksaena*, *Lichtheimia*
Glomeromycota (Schüβler *et al.*, 2001) syn. Glomeromycotina within Mucoromycta	Endomycorrhizal, except *Geosiphon*, which forms a symbiosis with cyanobacteria	Coenocytic hyphae, able to perform anastomosis; multinucleated spores; asexually formed chlamydospore-like spores are borne terminally, laterally, or intercalary on specialized hyphae; form specialized haustoria-like branched structures termed arbuscular mycorrhizae to interact with the host	
Diversisporales (Schüβler *et al.*, 2001)	Endomycorrhizal	Fungi hypogeous, forming endomycorrhizae with arbuscules, often lacking vesicles; with or without hypogeous auxiliary cells; forming either complex spores produced within a sporiferous saccule, complex spores developing from a bulbous base on the sporiferous hypha, or glomoid spores	*Acaulaspora*, *Gigaspora*, *Diversispora*
Glomerales (Schüβler *et al.*, 2001)	Endomycorrhizal	Fungi mostly hypogeous, sometimes epigeous, forming endomycorrhizae or mycorrhiza-like symbioses with spores, vesicles or arbuscules in plants; hyphae of vegetative mycelium mostly non-septate; asexual reproduction by glomoid spores, mainly terminal, but sometimes intercalary; spores solitary or formed in clusters, or in sporocarps	*Glomus*, *Rhizophagus*, *Funneliformis*
Paraglomerales (Schüβler *et al.*, 2001)	Endomycorrhizial	Fungi hypogeous, forming endomycorrhizae with arbuscules and intraradical mycelium, rarely with vesicles; non-pigmented glomoid spores	*Paraglomus*
Archaeosporales (Schüβler *et al.*, 2001)	Endomycorrhizal, except *Geosiphon*, which forms a symbiosis with cyanobacteria	Fungi hypogeous, forming endocytosymbioses with photoautotrophic prokaryotes, or endomycorrhizal; with or without vesicles; spores lacking pigmentation or reaction to Melzer's reagent; glomoid spores formed singly or in loose clusters on the soil, acaulosporoid complex spores formed singly in the soil; dense spore clusters unknown	*Archaeospora*, *Ambispora*, *Geosiphon*

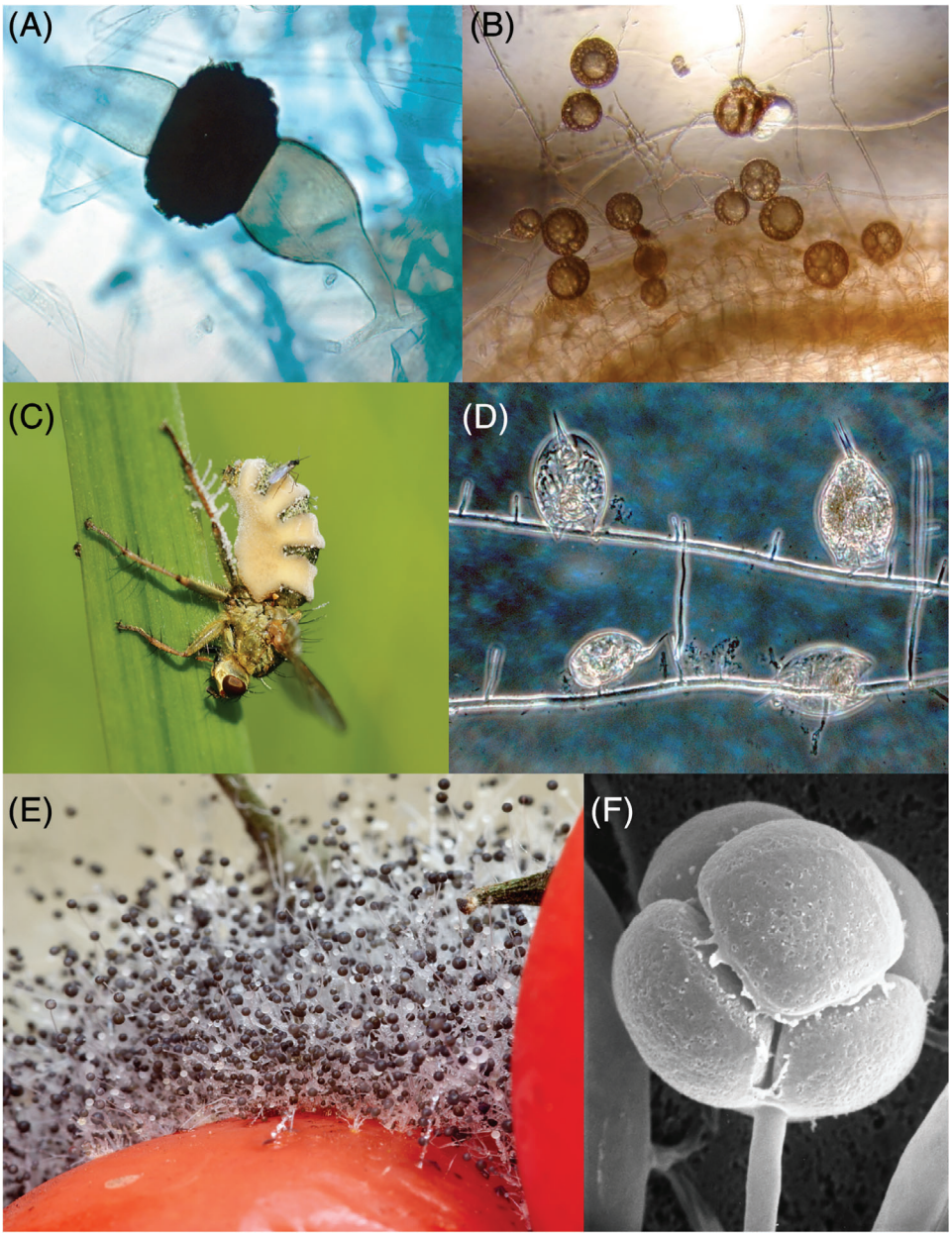

Fig. 4. Diversity of zygomycetous Fungi. (A) Zygospore from *Rhizopus stolonifer* (Mucorales, Mucoromycotina). Zygospores are naked sexual spores formed in the intersection of two mating hyphae in both Zoopagomycota and Mucoromycota. Original photograph by George Barron. Licensed for non-commercial academic and research use only. (B) Mycelium and multinucleated spores from *Rhizophagus intrarradices* (Glomerales, Glomeromycotina) growing in association with a plant root, appearing as a foamy structure in the lower part of the picture. The spores, appearing as dark brown globular structures, contain multiple nuclei that are thought to form a chimeric population (heterokaryon). Original photograph by Banco de Glomeromycota in vitro, CC BY-NC-ND 2.5 AR license. (C) *Entomophthora muscae* (Entomophthorales, Entomophthoromycotina) growing in a fly. The Entomophthorales include mostly entomopathogenic species that form an unwalled coenocytic mycelium that invades the host body before killing it. Original photograph by Hans Hillewaert, CC BY-SA 4.0 license. (D) Hyphae from *Zoophagus insidians* (Zoopagales, Zoopagomycotina) attacking a group of rotifers. Zoopagales is a group of parasitic fungi that mostly infect other fungi, protozoans and microinvertebrates. Original photograph by George Barron. Licensed for non-commercial academic and research use only. (E) Pin mould [probably *Rhizopus stolonifer* (Mucorales, Mucoromycotina)] growing on a tomato. Most members of the mucorales are fast-growing saprotrophs that present very large sporangia, appearing here as dark globose structures at the end of long aerial hyphae. Original photograph by Wikipedia user Calimo, CC BY-SA 3.0 license. (F) Scanning electron micrograph of a *Mortierella hyalina* (Mortierellales, Mortierellomycotina) sporangium. Members of the Mortierellomycotina have similar ecologies to Mucorales, but they can be easily differentiated by the absence of an inflated base to their sporangia (columella). Original photograph by flickr user ZygoLife Research Consortium, CC BY-SA 2.0 license.

Sigmoideomycetaceae) (Benny *et al.*, 2016). Several members of the Cochlonemataceae are endoparasites of amoebae or small animals, requiring engulfment by phagocytosis or ingestion by their host (Benny *et al.*, 2014). Inside the host, they grow as a poorly developed thallus. The remainder of the subphylum grow as a mycelium, often with a foamy appearance, use sticky substances to attach the host and produce haustoria to penetrate them (Duddington, 1956; Saikawa, 2011; Benny *et al.*, 2014). Most species show a narrow host range. Septa can be found in some genera (e.g. *Euryancale*, *Cystopage*). Both sexual and asexual spores have been described. The evolutionary relationships among the different families are not well resolved, mostly due to the difficulty of working with such small and usually unculturable fungi (Davis *et al.*, 2019*b*). Additionally, molecular analyses suggest that members of this clade show high evolutionary rates (Ahrendt *et al.*, 2018; Davis *et al.*, 2019*a*), and some of the most commonly used primers for barcode sequences of fungi or eukaryotes work poorly for this group (Tedersoo & Lindahl, 2016). This amplification problem is caused by their unusually long internal transcribed spacer (ITS) sequences, so the recent development of more-specific primers (Lazarus *et al.*, 2017) will help the study of these fungi to catch up with the rest of the kingdom. Finally, phylogenetic evaluation of genera in the Piptocephalidaceae (*Piptocephalis*, *Syncephalis*, *Kuzuhaea*) (Lazarus *et al.*, 2017), Zoopagaceae (*Zoopage*, *Zoophagus*, *Acaulopage*) and Cochlonemataceae (*Cochlonema*) (Lazarus *et al.*, 2017; Reynolds *et al.*, 2019) suggests that morphological characters might be insufficient for species or even genus delimitation in this subphylum and thus a large cryptic diversity is to be expected.

(*c*) *Kickxellomycotina*

Kickxellomycotina was created as a subphylum unifying several poorly studied fungal groups united by the presence of septated mycelia that present unique septal pores with a lenticular plug (Tanabe *et al.*, 2004; Hibbett *et al.*, 2007; Benny *et al.*, 2014). The morphology of these pore plugs, as well as the characteristics of the sporangia are diagnostic traits for the main groups within the subphylum (Tretter *et al.*, 2014). The group comprises four recognized orders (Kickxellales, Harpellales, Asellariales and Dimargaritales) plus several genera of still unresolved phylogenetic placement (*Ramicandelaber*, *Barbatospora*, *Orphella*, *Spiromyces* and *Mycoëmilia*) (Tretter *et al.*, 2013, 2014). New orders or higher taxonomical assignation for the *Ramicandelaber* and *Spiromyces* + *Mycoëmilia* clades have been proposed but have yet to find support (Benny *et al.*, 2016; Tedersoo *et al.*, 2018). Harpellales, Asellariales, *Orphella*, and *Barbatospora* are fungi with poorly developed thalli that are found in association with the gut of several groups of arthropods. Dimargaritales and *Martensella* (Kickxellales) are mycoparasites. The rest of Kickxellales, *Spiromyces*, *Mycöemilia* and *Ramicandelaber* grow as saprobes. The genus *Coemansia* (Kickxellaceae, Kickxellales) (Chuang *et al.*, 2017), a dung-associated saprotroph with intrincate asexual structures, was the first sequenced Kickxellomycotina (Chang *et al.*, 2015). The placement of some orders within the group has been difficult due to the existence of long-branch-attraction artefacts in molecular phylogenies (e.g. in Dimargaritales) (Tanabe *et al.*, 2000; Tretter *et al.*, 2013) and the difficulty of obtaining DNA for several lineages. The saprotrophic members of the group are common in soil and dung (Benny *et al.*, 2014).

(*d*) *Future prospects in the Zoopagomycota*

The phylogenetic placement and definition of Zoopagomycota has been controversial. They were originally placed within the Zygomycota, a group that was later shown to be paraphyletic, comprising up to 10 independent orders whose relationships were uncertain (Benny *et al.*, 2014). In this context, the relationship between Zoopagomycotina and Kickxellomycotina was established (White *et al.*, 2006; Hibbett *et al.*, 2007; Spatafora *et al.*, 2016). Finally, the monophyly of Entomophthoromycotina, as well as its relationships with the rest of the phylum were resolved, and the phylum Zoopagomycota was proposed (Spatafora *et al.*, 2016). In addition to the described groups, environmental sequencing studies have described Clade GS19, which may represent a novel lineage distinct from any of the subphyla (Spatafora *et al.*, 2016) or a distinct lineage within Kickxellomycotina (Tedersoo *et al.*, 2017). Given the general association of these fungi with metazoans and other organisms in soil, we expect their presence in soil to be low in terms of biomass, and associated with their hosts. This seems to be the case for rainforest (Tedersoo *et al.*, 2018) and prairie soils (Dunthorn *et al.*, 2017). Contrary to this assumption, however, there are reports of high abundance of sequences from amoebophagous fungi (genus *Kuzuhaea*, Zoopagales) in permafrost soils, suggesting that these microfungi are indeed highly abundant in at least certain environments (Penton *et al.*, 2013). The known diversity of their usual hosts (i.e. amoebae, insects, fungi and nematodes) suggests that the undescribed diversity of these fungi might be very large, particularly considering that many of these interactions seem to be quite specific. Outside parasitic relationships, members of this group [*Basidiobolus* (Basidiobolomycetes), *Coemansia*, (Kickxellales)], together with *Mortierella* (Mortierellomycotina), were reported to be enriched on the surfaces of two species soil acari compared to the surrounding soil, forming distinct communities for each species (Werner, Peršoh, & Rambold, 2018). While their small size imposes challenges to traditional sequencing approaches, they are prime candidates for single-cell sequencing-based techniques. Using the latter methods, several genomes in these lineages have been sequenced recently (Ahrendt *et al.*, 2018).

(2) Glomeromycota

Virtually all known members of this phylum live as obligate symbionts of land plants, forming a particular type of symbiosis termed arbuscular mycorrhizae. Glomeromycota was separated from the rest of Zygomycota based on early ribosomal protein phylogenies (Schüβler, Schwarzott,

& Walker, 2001). The fungus mycelia grow inside the root of the plant, penetrating the cells of the host. The mycelium is always non-septate and presents anastomoses (Redecker & Schüßler, 2014). Members of this group have 24-ethyl-cholesterol as the main membrane sterol, apparently lacking ergosterol (Weete *et al.*, 2010). The fungus helps the plant with the acquisition of phosphorus, nitrogen and water in exchange for photosynthesis-derived metabolites. Functionally similar associations exist for members of Mucoromycota, Ascomycota and Basidiomycota, but Glomeromycota is by far the most common symbiont group associating with nearly three-quarters of land plants (Bidartondo *et al.*, 2011). Four orders are recognized within the Glomeromycota (Paraglomerales, Archaeosporales, Diversisporales and Glomerales) that include 11 families and around 230 morphospecies (Stürmer, 2012). Their spores are multinucleated (with up to hundreds of nuclei that are often genetically distinct populations), very large, and filled with lipid and protein globules. Spore morphology defines the different groups.

Geosiphon pyriforme (Geosiphonaceae, Archaeosporales) is the only member of the phylum that does not form arbuscular mycorhizae (Gehrig, Schüßler, & Kluge, 1996). It grows as a symbiont of colonies of cyanobacteria in the genus *Nostoc* in a fashion that some authors have considered functionally similar to a lichen (; Kluge *et al.*, 2002). The symbiosis is photosynthetically active (Kluge, Mollenhauer, & Mollenhauer, 1991) and is able to fix atmospheric nitrogen (Kluge *et al.*, 1992). However, the ultrastructure of the symbiosis is more akin to arbuscular mycorrhizae than to a prototypical lichen (Schüßler *et al.*, 2007).

Earlier studies placed Glomeromycota as the sister clade to Dikarya (Ascomycota + Basidiomycota + Entorrhizomycota) (Schüβler *et al.*, 2001; Lutzoni *et al.*, 2004; White *et al.*, 2006), while most recent phylogenies place them as sister to or within Mucoromycota (Liu, Hodson, & Hall, 2006; Nadimi *et al.*, 2012; Lin *et al.*, 2014; Spatafora *et al.*, 2016). Spatafora *et al.* (2016) classified this group as subphylum Glomeromycotina within Mucoromycota. However, we consider that elevation to phylum status is justified by their phenotypical peculiarities and historical use, and that such nomenclature is compatible with either phylogenetic scenario. The discovery of several novel lineages (see Section V) will eventually force taxonomists to reevaluate the Glomeromycota and Mucoromycota, but we consider it premature to merge these two groups before resolving the phylogenetic placement of these new lineages on the fungal tree of life. As biotrophic organisms, they cannot be grown axenically, and must be cultured using experimentally tractable plants. In general terms, most described species show low host specificity and low endemism (Davison *et al.*, 2015), although is highly likely that sampling and identification methodologies are biased towards generalist and highly resilient species (Ohsowski *et al.*, 2014). Environmental studies show that this group is ubiquitous and probably much more diverse than previously thought (Ohsowski *et al.*, 2014; Tedersoo *et al.*, 2017). Solid indirect evidence of sexual recombination has been described, although no sexual structures have ever be observed (Sanders, 2011; Tisserant *et al.*, 2013).

(3) Mucoromycota

Mucoromycota comprises the largest and best-studied group of zygomycetous fungi. Most species grow as saprobes, with some species being non-haustorial parasites of plants and other fungi, or ectomycorrhizal. It includes two subphyla: Mortierellomycotina and Mucoromycotina (Hoffmann, Voigt, & Kirk, 2011; Benny *et al.*, 2014; Spatafora *et al.*, 2016). They grow as coenocytic and anostomosing hyphae. Certain members of this phylum are important in the food industry as causes of food spoilage (Filtenborg, Frisvad, & Thrane, 1996; Moss, 2008; Garnier, Valence, & Mounier, 2017) or in the preparation of certain fermented foods (Londoño-Hernández *et al.*, 2017). Some can also cause rare but highly invasive infections in humans and animals (Kwon-Chung, 2012; Fisher, Gow, & Gurr, 2016; Serris *et al.*, 2019). Several members of this lineage, specially the orders Mucorales (Mucoromycotina) and Mortierellales (Morteirellomycotina) are used in industrial fermentations for the production of chitosan, lipids or carotenoids (Conti *et al.*, 2001; Kuzina & Cerdá-Olmedo, 2007; Papanikolaou *et al.*, 2007; Karimi & Zamani, 2013).

(*a*) *Mortierellomycotina*

Mortierellomycotina are morphologically and ecologically similar to the rest of the group, but their phylogenetic positioning has been historically convoluted (Rosewich & Kistler, 2000; Voigt & Wöstemeyer, 2001; Tanabe *et al.*, 2005; Kwaśna, Ward, & Bateman, 2006; Nadimi *et al.*, 2012; Wagner *et al.*, 2013). The subphylum includes one family, 13 genera and more than 100 currently recognized species (Wagner *et al.*, 2013). Mortierellomycotina are diferentiated from Mucoromycotina by the morphology of the zygospore, and the absence of a columella, which is a basally inflated sporangiophore. Many produce a characteristic colony morphology and garlic-like odour when grown in culture. The elevation to subphylum for this group is based exclusively on phylogenetic analyses (White *et al.*, 2006; Hoffmann *et al.*, 2011; Spatafora *et al.*, 2016) that suggest that it constitutes a phylogenetically distinct lineage, sister to Mucoromycota. Most species of this clade are ascribed to the paraphyletic genus *Mortierella* (Petkovits *et al.*, 2011). The group also includes some specialized forms, such as *Aquamortierella*, which is found only in aquatic habitats (Embree & Indoh, 1967).

(*b*) *Mucoromycotina*

Mucoromycotina includes two orders: Endogonales and Mucorales. It is noteworthy that many older references use Mucorales in a sense that roughly equates to the modern circumscription of Mucoromycota or Mucoromycotina. Some authors recognize an additional order, Umbelopsidales, that includes the single family Umbelopsidaceae (Spatafora *et al.*, 2016). Endogonales comprises a single family, four genera

and about 30 species, while Mucorales spans 14 families comprising 56 genera and around 300 species (Benny *et al.*, 2014). Some members of Endogonales form ectomycorrhizal associations with some plants, and in particular with certain lineages of liverworts (Bidartondo *et al.*, 2011; Field *et al.*, 2015; Orchard *et al.*, 2017). Compared to most fungi, cell walls of Mucoromycotina are known to contain chitosan, a deacetylated form of chitin, as the main structural component (Ruiz-Herrera & Ortiz-Castellanos, 2010; Mélida *et al.*, 2015). They also present an extrusion of the sporangiophore termed a columella that is synapomorphic for the subphylum. Porous, plasmodesmata-containing septa may appear in reproductive structures and senescent hyphae. Most species are saprotrophs, and occasionally can be facultative parasites of animals, plants and other fungi. At least three genera (*Dicranophora*, *Spinellus* and *Syzygites*) are obligate parasites of mushrooms (Benny *et al.*, 2014).

(*c*) *Future prospects in the Mucoromycota*

Environmental studies reveal that Mucoromycotina and Mortierellomycotina are ubiquous in most environments and suggest that a large fraction of the diversity in both subphyla remains unexplored (Tedersoo *et al.*, 2014, 2017; Ziaee *et al.*, 2016). As mentioned above, the relationship with other phyla is debated (Liu *et al.*, 2006; Nadimi *et al.*, 2012; Lin *et al.*, 2014; Spatafora *et al.*, 2016). Several genera have recently been assigned to the Mucoromycota based on molecular studies, which probably implies that a taxonomic overhaul of the Mucoromycota and the establishment of novel orders or classes is necessary. These genera and their phylogenetic affiliations are discussed further in Section V.

IV. DIKARYA

Dikarya is by far the most species-rich and best-studied group of Fungi. It includes two main phyla, Basidiomycota and Ascomycota. Additionally, a small group of root endophytes has recently been proposed to represent a third phylum, Entorrhizomycota (see Section V). Dikarya are characterized for a sexual cycle that includes hyphal fusion uncoupled with meiosis, which in turn produces hyphae that contain two independent nuclear populations (dikaryotic hyphae). Most also present septated hyphae, ergosterol as the membrane sterol, and several lineages are even able to form multicellular reproductive or vegetative structures. Figure 5 provides examples of Basidiomycota, while Fig. 6 does the same for Ascomycota, while the main lineages of these groups are listed in Tables 4 and 5, respectively.

(**1**) **Basidiomycota**

Basidiomycota is the second most species-rich phylum of Fungi with nearly 32,000 described species (Hibbett *et al.*, 2007; Adl *et al.*, 2012, 2018; Zhao *et al.*, 2017), which present a wide array of lifestyles and cell-organization strategies. Basidiomycota comprise the most complex fungi in terms of cell cycle (e.g. *Puccinia*) and multicellularity (e.g. the mushroom-forming fungi, particularly the genus *Armilliaria*). The main characteristic of the group is the production of specialized club-like cells called basidia, that usually produce four sexual spores (Hibbett *et al.*, 2007; Adl *et al.*, 2012; McLaughlin & Spatafora, 2014). Mating usually implies anastomosis between the two mating hyphae and formation of a dikaryon – hyphae with two stable populations of nuclei. The nuclei in the dikaryon remain in association before undergoing karyogamy and meoisis to produce the basidiospores. Hyphae, when present, are septate. In some of the groups, septa present dolipores – dome-shaped modified endoplasmic reticulum (parenthesome). The formation of basidia is shared with the Entorhizomycota (see Section V.5). The phylum Basidiomycota contains at at least three well-defined lineages: Pucciniomycotina, Ustilagomycotina, and Agaricomycotina. Most phylogenies recover Ustilaginomycotina as sister to Agaricomycotina, with Pucciniomycotina as the earliest diverging branch. This relationship remains debated as it seems to be greatly influenced by methodological biases (Prasanna *et al.*, 2019). Wallemiomycotina is a recently recognized subphylum that includes a few genera (*Wallemia*, *Basidioascus*, *Geminibasidium*) of thermoresistant and xerotolerant moulds or yeast-like fungi (Zalar *et al.*, 2005; Padamsee *et al.*, 2012; Zajc *et al.*, 2013; Nasr *et al.*, 2014). The ultrastructure of the septal pore in *Wallemia* is similar to members of Tremellomycetes (Zalar *et al.*, 2005; Matheny *et al.*, 2006; Zhao *et al.*, 2017). The phylogenetic positioning of this clade is currently uncertain (Fig. 7). Some phylogenies have placed them as the earliest branching class (Wallemiomycetes) within Agaricomycotina (or, equally, as sister to Agaricomycotina) (Matheny *et al.*, 2006; Padamsee *et al.*, 2012; Nguyen, Nickerson, & Seifert, 2013; Zajc *et al.*, 2013; Nguyen *et al.*, 2015; Zhao *et al.*, 2017; Mishra, Choi, & Thines, 2018). Other phylogenies place them as sister to the other three subphyla (Matheny *et al.*, 2006; Wang *et al.*, 2014; Zhao *et al.*, 2017), with some studies reporting both topologies depending on the phylogenetic markers used, or as sister to Ustilaginomycotina (Bauer *et al.*, 2015; Tedersoo *et al.*, 2018). The largest differences stem from the use of ribosomal markers *versus* protein-coding genes, with genome-wide data sets preferentially supporting a sister relationship with Agaricomycotina. We here use the subphylum category, as it is compatible with either phylogenetic hypothesis. The three genera form two deeply divergent clades classified as distinct orders (McLaughlin & Spatafora, 2014) or classes (Nguyen *et al.*, 2013), with *Wallemia* as sister to *Basidioascus* + *Geminibasidium*. Finally, *Bartheletia paradoxa* is an enigmatic filamentous fungus with a unique septal structure, consisting of multiple plasmodema-like perforations, that lives in association with fallen leaves of *Ginkgo biloba* (Scheuer *et al.*, 2008). Recent phylogenomic analyses place *Bartheletia* as sister to Agaricomycotina + Wallemiomycotina (Mishra *et al.*, 2018). The latter authors suggest retaining Wallemiomycetes within the subphylum Agaricomycotina, and raising a new class Bartheletiomycetes

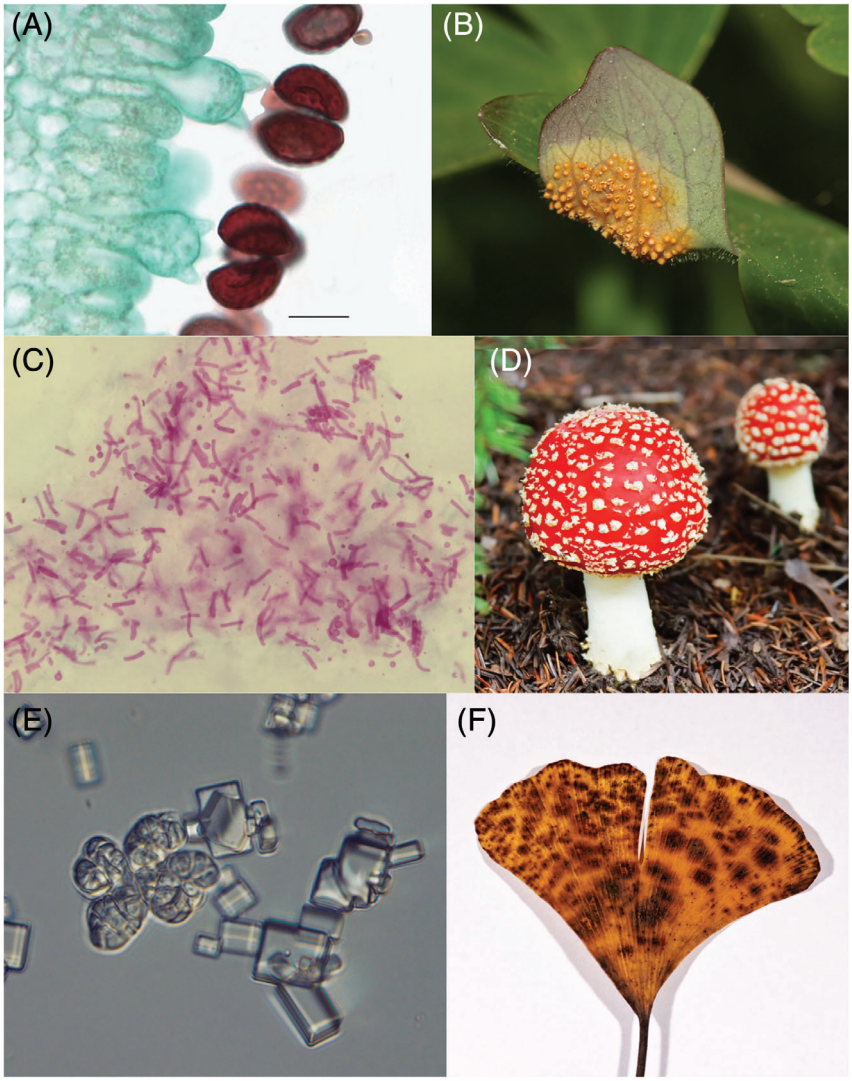

Fig. 5. Diversity of Basidiomycota. (A) Basidia from *Coprinus* (Agaricomycetes, Agaricomycotina). Basidia are reproductive structures formed by a cell attached to the (typically four) derived spores produced by meiosis, appearing here as dark structures. Original photograph by Wikipedia user Jon Houseman, CC BY-SA 3.0 license. (B) *Puccinia recondita* (Pucciniomycetes, Pucciniomycotina) growing on the back of a leaf. Pucciniomycetes are a diverse class of biotrophic plant pathogens within the Pucciniomycotina. Original photograph by flickr user Line Sabroe, CC BY 2.0 license. (C) Micrograph of a skin cell infected by *Malassezia furfur* (Malasseziomycetes, Ustilaginomycotina). Although most Ustilaginomycotina are plant pathogens, the genus *Malassezia* is commonly found in the skin of mammals. Original photograph in the public domain. (D) Fruiting bodies of *Amanita muscaria* (Agaricomycetes, Agaricomycotina), a poisonous mushroom famous for its bright white and red colour and its hallucinogenic properties. Original photograph in the public domain. (E) Micrograph of *Wallemia ichthyophaga* (Wallemiomycetes, Wallemiomycotina), appearing as a rounded mass. Wallemiomycetes contains a few species of highly extremotolerant fungi. *W. ichthyophaga* in particular requires high salinity to grow, as can be seen from the presence of cubic salt crystals in the picture. Photograph by Wikipedia user Anticicklon, CC BY-SA 3.0 license. (F) A *Ginkgo biloba* leaf covered by clustersof black *Bartheletia paradoxa* telia. *B. paradoxa* represents a divergent lineage that has probably co-evolved with Ginkgopsida, an ancient plant lineage of which there is only one extant species. Original photograph by flicker user AJC1, CC BY-SA 2.0 license.

to include *Bartheletia* (Mishra *et al.*, 2018) in that subphylum.

(*a*) *Pucciniomycotina*

There are more than 8,400 described species of Pucciniomycotina, classified in 10 classes (Agaricostilbomycetes, Atractiellomycetes, Classiculomycetes, Cryptomycocolacomycetes, Cystobasidiomycetes, Microbotryomycetes, Mixiomycetes, Pucciniomycetes, Spiculogloeomycetes and Tritirachiomycetes), 20 orders and 35 families (Aime *et al.*, 2006; Schell, Lee, & Aime, 2011; Wang *et al.*, 2015*b*,*c*). Some members of the group, particularly in the Pucciniomycetes, have very large genomes (Tavares *et al.*, 2014) and several

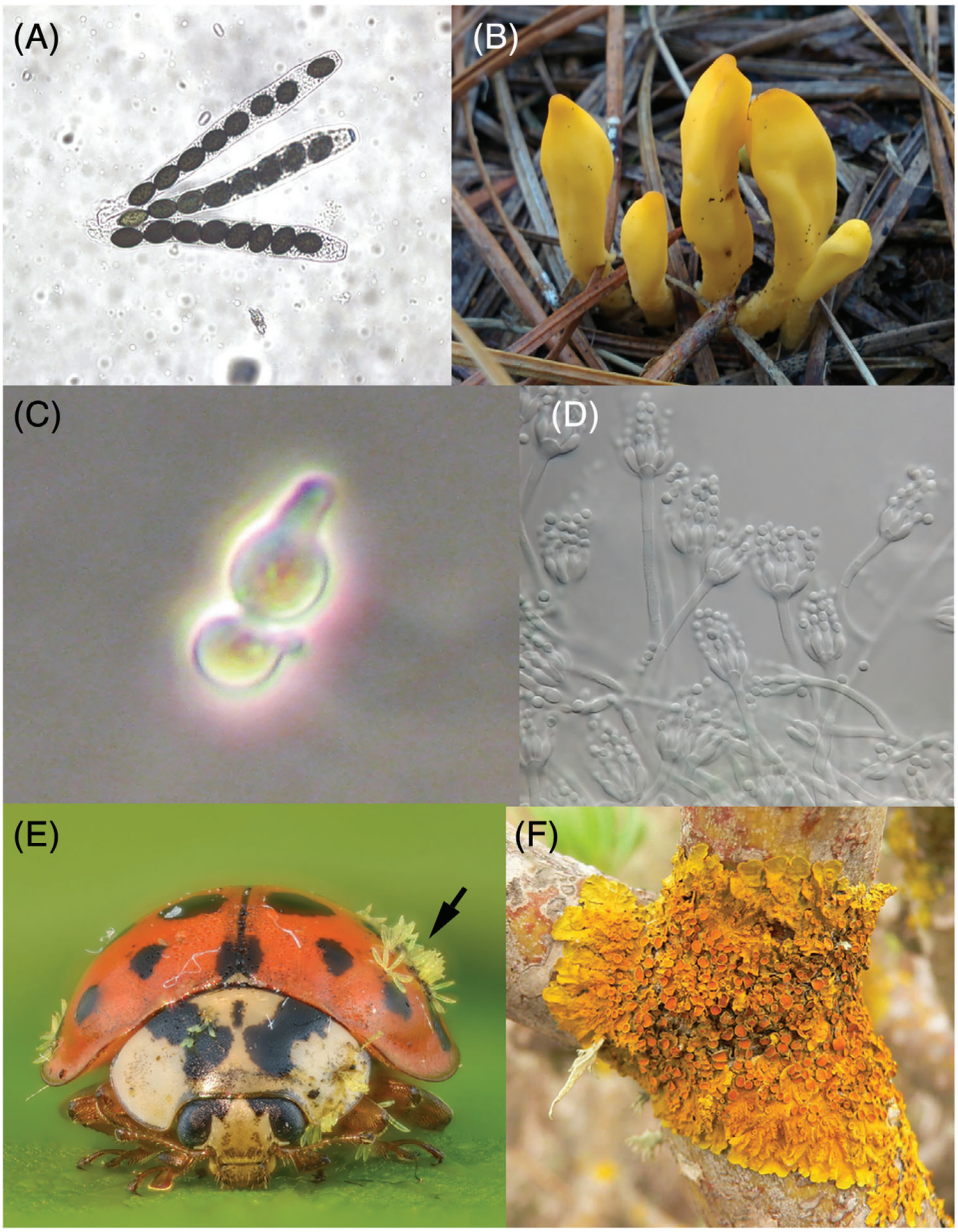

Fig. 6. Diversity of Ascomycota. (A) Asci from *Sordaria fimicola* (Sordariomycetes, Pezizomycotina). Asci are reproductive structures that enclose (typically four or eight) spores produced by meiosis, appearing here as dark structures. Original photograph by Wikipedia user CarmelitaLevin CC BY-SA 4.0 license. (B) Fruiting bodies of *Neolecta vitellina* (Neolectomycetes, Taphrinomycotina). Taphrinomycotina includes several lineages with a wide range of body plans, ranging from intracellular parasites to complex multicellular fungi. Original photograph by Mushroom Observer user gillow2e, CC BY-SA 3.0 license. (C) Mating cells (Shmoo) of *Saccharomyces cerevisiae*. Under the right conditions haploid cells enter the shmoo mating state and fuse with a mating cell of the opposite mating type, producing a diploid cell. The diploid cell can enter meiosis, producing an ascus with four spores, from which haploid cells germinate. Original photograph by Wikipedia user Pilarbini, CC BY-SA 4.0 license. (D) Micrograph of a group of conidia from *Penicillium spinulosum* (Eurotiomycetes, Pezizomycotina). *Penicillium* is a genus of cosmopolitan moulds that mostly propagate by producing high numbers of asexual conidiospores. Original photograph by Wikipedia user Medmyco, CC BY-SA 4.0 license. (E) Photograph of a ladybird infected with *Hesperomyces virescens* (Laboulbeniomycetes, Pezizomycotina), appearing here as light-coloured digitiform structures (see arrow). Laboulbeniales are a diverse order of fungi associated with arthropod surfaces that present determinate growth and separate sexes. Original photograph by flickr user Gilles San Martin, CC BY-SA 2.0 license. (F) *Xanthoria parietina*, a lichen, growing on a branch. In the picture, disk-like structures can be observed sprouting prefentially in the centre of the formation. These correspond with the apothecia, support tissues containing the asci. Original photograph by Wikipedia user Marianne Perdomo, CC BY-SA 2.0 license.

Table 4. Main lineages within Basidiomycota. Due to changes in the scope of certain historical clades, references might not refer to the initial published description of a clade but to more recent bibliography

Name	Main described lifestyles	Main traits	Representative genera
Pucciniomycotina (Adl *et al.*, 2012)	Unicellular and filamentous; biotrophic plant pathogens, insect parasites, saprobes, endophytes and mycorrhizal	Karyogamy typically in probasidium or teliospore, followed by meiosis commonly in a separate compartment; simple septal pores occluded by a pore; presence of mannose and absence of xylose as cell wall component; centrosome multilayered	
Tritirachiomycetes (Schell *et al.*, 2011)	Saprobes	Mycelial; uniperforate simple septa; conidiophores subhyaline to dematiaceous; teleomorph not known	*Tritirachium*
Mixiomycetes (Adl *et al.*, 2012)	Biotrophic parasites of ferns	Multinucleated hyphae and multiple spores produced simultaneously in sporogeneous cells	*Mixia*
Agaricostilbomycetes (Wang *et al.*, 2015*c*)	Saprotrophic yeast-like or dimorphic, mycoparasites	Dimorphic; fucose as cell wall carbohydrate component, septal pores without associated microbodies, aseptate basidiospores during germination and no colacosomes, teliospores, curved holobasidia, and radiate conidia; nucleoplasmic spindle-pole-body separation, metaphasic spindle-pole body intranuclear	*Agaricostylbum*, *Chionosphaera*, *Ruinenia*, *Jianyunia*, *Kondoa*
Cystobasidiomycetes (Adl *et al.*, 2012; Wang *et al.*, 2015*c*; Oberwinkler, 2017)	Mycoparasites, saprobes	Absence of fucose in cell wall; cytoplasmic spindle-pole-body separation; metaphasic spindle-pole body intranuclear; presence of mycosporines	*Cystobasidium*, *Bannoa*, *Erythrobasidium*, *Naohidea*, *Sakaguchia*, *Cyrenella*
Microbotryomycetes (Adl *et al.*, 2012; Wang *et al.*, 2015*c*; Oberwinkler, 2017)	Biotrophic plant pathogens, yeast-like	Presence of colacosomes and septal pores without microbodies; etaphasic spindle pole bodies intranuclear	*Microbotryum*, *Heterogastridium*, *Mastigobasidium*, *Sporidiobolus*
Classiculomycetes (Adl *et al.*, 2012)	Aquatic, probably mycoparasite	Septal bodies associated with microbodies and tremelloid haustorial cells	*Classicula*, *Jaculispora*
Cryptomycocolacomycetes (Adl *et al.*, 2012)	Mycoparasites	Colacosomes and septal pores with microbodies	*Cryptomycocolax*
Atractiellomycetes (Kottke *et al.*, 2010;Adl *et al.*, 2012 ; Aime *et al.*, 2014)	Saprobes, mycorrhizae with orchids	Presence of symphlechosomes; filamentous; some genera form fruiting bodies	*Atractiella*, *Saccoblastia*, *Helicogloea*, *Hobsonia*
Pucciniomycetes (Adl *et al.*, 2012; Aime *et al.*, 2014)	Biotrophic plant pathogens, insect parasites, mycoparasites	Metaphasic intermeiotic spindle-pole-body duplication	*Puccinia*, *Septobasidium*, *Melampsora*, *Cronartium*, *Pachnocybe*, *Platygloea*
Spiculogloeomycetes (Wang *et al.*, 2015*c*)	Mycoparasitic, saprobe	Defined phylogenetically; teleomorphic members that may form tremelloid haustorial cells	*Spiculogloea*, *Mycogloea*, *Sporobolomyces*
Ustilagomycotina (Adl *et al.*, 2012)	Unicellular and filamentous; saprobes or biotrophic plant pathogens	Mostly yeasts or dimorphic yeasts; glucose-rich cell walls; simple septal pores	
Malasseziomycetes (Wang *et al.*, 2014)	Lipophylic fungi; associated with vertebrate skin, commonly found in the environment	Cells are globose, ovoid or cylindrical; budding is typically monopolar, enteroblastic and percurrent; cell wall multilamellate, inner layer of the cell wall corrugated with a groove spiralling from the bud site; lipid dependent or lipophilic	*Malassezia*
Exobasidiomycetes (Adl *et al.*, 2012)	Plant biotrophic pathogens, saprobes, animal parasites	Presence of interaction zones and no intracellular hyphal coils; probably paraphyletic	*Ceraceosorus*, *Exobasidium*, *Doassansia*, *Entyloma*

Table 4. *(Cont.)*

Name	Main described lifestyles	Main traits	Representative genera
Ustilaginomycetes (Adl *et al.*, 2012)	Biotrophic plant pathogens	Glucose as main cell wall carbohydrate, xylose absent; parenthesomes absent from septal pores; centrosomes globosed, unlayered	*Ustilago*, *Urocystis*, *Floromyces*, *Tilletia*
Moniliellomycetes (Wang *et al.*, 2014)	Saprobes, some species are xerophilic	Sexual morph unknown; smooth or velvety colonies, greyish to olivaceous black; budding cells ellipsoidal; true hyphae disarticulate with arthroconidia;. pseudohyphae and chlamydospores may be present; multi-lamellar cell wall; hyphal septa typically possess dolipores with an arch of endoplasmic reticulum, micropore-like structures may also be present	*Moniliella*
Agaricomycotina (Adl *et al.*, 2012)	Filamentous, yeasts or dimorphic yeasts; saprobes, plant parasites and ectomycorrhizal; also endophytes, mycoparasites, amoebophagous, symbionts and lichens	Many produce macroscopic fruiting bodies; pore septa with endoplasmic reticulum-derived structures; xylose in cell wall; B type 5S rRNA	
Agaricomycetes (Adl *et al.*, 2012)	Filamentous fungi; saprobes, plant parasites, mycorrhizal; also endophytes, mycoparasites, amoebophagous, symbionts and lichens	Often presenting macroscopic and complex fruiting bodies; commonly found as a dikaryon; many present lignin-degrading capabilities	*Amanita*, *Agaricus*, *Auricularia*, *Geastrum*, *Rhizoctonia*, *Trametes*, *Lentinula*
Dacrymycetes (Adl *et al.*, 2012)	Wood-decaying saprobes	Gelatinous fruiting bodies; basidia furcate, rarely unisporous; parenthesomes unperforated	*Dacryopinax*, *Cerinomyces*
Tremellomycetes (Adl *et al.*, 2012)	Saprobes, mycoparasites	Dimorphic, fruiting body gelatinous or absent; basidia septate or non-septate; parenthesomes sacculate or absent	*Tremella*, *Cryptococcus*, *Filobasidium*, *Mrakia*
Wallemiomycotina (Nguyen *et al.*, 2013) syn. Wallemiomycetes, within Agaricomycotina	Extremotolerant, filamentous or yeast-like	Basidiomata absent; basidiospores produced by some genera; arthroconidial or basauxic anamorphs are produced in some species	*Wallemia*, *Basidioascus*, *Geminibasidium*
Bartheletiomycetes (within Agaricomycotina) (Scheuer *et al.*, 2008; Mishra *et al.*, 2018) syn. Bartheletiomycotina	Associated with fallen leaves of *Ginkgo biloba*	Septa with multiple plasmodesma-like perforations; sexual reproduction by thick walled teliospores with longitudinally septated basidia	*Bartheletia*

Table 5. Main lineages within Ascomycota. Due to changes in the scope of certain historical clades, references might not refer to the initial published description of a clade but to more recent bibliography

Name	Main described lifestyles	Main traits	Representative genera
Taphrinomycotina (Adl *et al.*, 2012) syn. Archiascomycetes (obsolete)	Filamentous or yeast; plant pathogens, saprotrophs, endophytes, animal pathogens	Asci produced from binucleate cells; do not form croziers or interascal tissue	
Taphrinomycetes (Adl *et al.*, 2012)	Biotrophic plant pathogens or saprotrophic yeasts	Poorly developed mycelium or yeast-like; dikaryotic mycelium infective, develops directly into asci globose with eight spores; yeast-like monokaryotic anamorph	*Taphrina*, *Protomyces*, *Saitoella*
Archaeorhizomycetes (also known as Soil Clone Group I) (Rosling *et al.*, 2011)	Root endophytes; seems to have a large and unexplored diversity in soils	Filamentous, simple septa	*Archaeorhyzomyces*
Schizosaccharomycetes (Adl *et al.*, 2012)	Saprotrophic yeasts on sugary substrates; sometimes dimorphic	Unicellular fungi dividing by fission; mycelium absent or poorly developed; sexual reproduction by fusion of two vegetative cells to form an ascus; karyogamy and meiosis inside the ascus to produce four nuclei, which might divide to form eight	*Schizosaccharomyces*
Pneumocystomycetes (Adl *et al.*, 2012)	Obligate pulmonary extracellular parasite of mammals	Thin cell wall, irregular shape; sexual reproduction initiated by fusion of two cells followed by karyogamy and cyst wall formation; cholesterol as main membrane sterol	*Pneumocystis*
Neolectomycetes (Landvik *et al.*, 2003; Adl *et al.*, 2012)	Unclear; probably saprobe or root associated	Filamentous, forming stalked fruiting bodies; cylindrical asci formed from binucleate cells that undergo karyogamy, meiosis, and one mitotic division to produce eight cylindrical ascospores; septa with Woronin body	*Neolecta*
Saccharomycotina (Adl *et al.*, 2012) syn. Hemiascomycota (obsolete)	Saprobes, commensals, extremotolerants and parasites; most are yeasts	Yeast-like or poorly developed mycelium; sexual reproduction by fusion of vegetative cell; ascomata absent; asci separated by endomembranes; genome reduction; several groups have modifications in their genetic code	*Saccharomyces*, *Candida*, *Yarrowia*, *Zygosaccharomyces*, *Pichia*, *Lipomyces*
Pezizomycotina (Adl *et al.*, 2012) syn. Euascomycota (obsolete)	Mostly filamentous; saprobes and lichens; also plant necrotrophic or biotrophic parasites, animal parasites, mycorrhizal, endophytes, amoebophagous and extremophiles	Filaments present septa with Woronin bodies; asci protected by multicelullular structures	
Arthoniomycetes (Adl *et al.*, 2012)	Lichen forming or saprobes	Ascomata usually apothecial; interascal tissue of branched paraphysoids in a gel matrix; asci thick-walled, fissitunicate	*Arthonia*, *Melaspilea*, *Opegrapha*, *Roccella*
Coniocybomycetes (Prieto *et al.*, 2013)	Lichen forming	Apothecia stalked, excipulum poorly to well developed, formed as a continuation of the stalk tissue; capitulum spherical to obconical; mazaedium present, brown to pale; asci cylindrical, ellipsoid, or irregular, dissolving at an early stage, forming from ascogenous hyphae with or without croziers, either singly or in chains; spores simple, spherical, or ellipsoidal, or rarely cylindrical with 1–5 septa, pale to brown, smooth or with a verrucose or cracked ornamentation	*Coniocybe*, *Sclerophora*

Table 5. *(Cont.)*

Name	Main described lifestyles	Main traits	Representative genera
Dothideomycetes (Adl *et al.*, 2012)	Saprobes, extremotolerant black fungi, plant pathogens, occasionally lichen forming	Ascomata variable, formed lysigenously from stromatic tissue; asci cylindrical to saccate, thick-walled, fissitunicate, rarely with apical structures; ascospores septate or muriform	*Mycosphaerella*, *Cladosporium*, *Venturia*, *Holmiella*, *Botryosphaeria*, *Pseudogymnoascus*
Eurotiomycetes (Hibbett *et al.*, 2007; Adl *et al.*, 2012)	Saprobes, extremotolerant black fungi, animal parasites, plant pathogens, occasionally lichen forming	Morphologically diverse, delimited by phylogenetic criteria	*Aspergillus*, *Penicillium*, *Capronia*, *Endocarpon*, *Onygena*, *Mycocalicium*
Geoglossomycetes (Adl *et al.*, 2012)	Saprobes	Fruiting bodies cylindrical, dark coloured, 2–8 cm long; septate ascospores, commonly pigmented	*Geoglossum*, *Trichoglossum*
Laboulbeniomycetes (Adl *et al.*, 2012)	Ectoparasites of insects and other terrestrial or aquatic arthropods, mycoparasites	Mycelium absent or poorly developed; basal haustorium; ascomata perithecial, usually surrounded by complex appendages; ascospores two-celled, elongated, one end adapted to attach to the host	*Laboulbenia*, *Herpomyces*, *Pyxidophora*, *Ceratomyces*, *Cochliomyces*
Lecanoromycetes (Adl *et al.*, 2012)	Lichen forming, occasionally saprobes	Asci fissitunicate, thick-walled, with thickened cap-like appendage; septate ascospores	*Acarospora*, *Cladonia*, *Candelaria*, *Graphis*, *Pertusaria*
Lichinomycetes (Adl *et al.*, 2012)	Lichen forming with cyanobacteria	Ascomata apothecial, setose and fleshy; asci simple, thin-walled, usually surrounded by a gelatinous layer; thallus usually gelatinous	*Lichina*, *Peltula*, *Eremithallus*
Leotiomycetes (Adl *et al.*, 2012)	Saprobes, plant pathogens, occasionally lichen forming	Ascomata apothecial, discoid, cleistothecial, elongated or absent, usually fleshy, commonly hairy or with appendages; thin-walled peridium; asci typically inorpeculate, cylindrical, thin-walled	*Erysiphe*, *Botryotinia*, *Sclerotinia*, *Thelebolus*, *Leotia*, *Macroderma*
Orbiliomycetes (Adl *et al.*, 2012)	Filamentous saprobes; amoeba and nematode trapping	Ascomata apothecial, small, waxy, translucent or lightly pigmented; interascal tissue of simple paraphyses, usually with knob-like apices, united by a matrix; many species form specialized trapping structures	*Orbilia*, *Arthrobotrys*, *Dactylellina*
Pezizomycetes (Adl *et al.*, 2012)	Saprobes, ectomycorrhizal or biotrophic plant pathogens	Ascomata apothecial or cleistothecial, usually visible with unaided eye, leathery or fleshy and often brightly pigmented; interascal tissue present; asci not fissitunicate, usually elongated, cylindrical, thin-walled, without wall thickening or apical apparatus, with operculum or vertical slit, forcibly discharging ascospores; cleisthotecial species present globose asci, lack operculum or vertical slit and do not discharge ascospores; scospores usually ellipsoidal or globose, aseptate	*Peziza*, *Tuber*, *Pyronema*, *Ascobolus*
Sordariomycetes (Adl *et al.*, 2012)	Saprobes, plant pathogens, animal parasites, mycoparasites, endophytes, occasionally lichen forming	Morphologically diverse, delimited by phylogenetic criteria	*Neurospora*, *Colletotrichum*, *Nectria*, *Cordyceps*, *Hypocrea*, *Bertia*, *Ceratocystis*, *Ophiostoma*
Xylonomycetes (Gazis *et al.*, 2012)	Endophytes, beetle-associated symbionts	Defined by phylogenetic criteria	*Xylona*, *Symbiotaphrina*

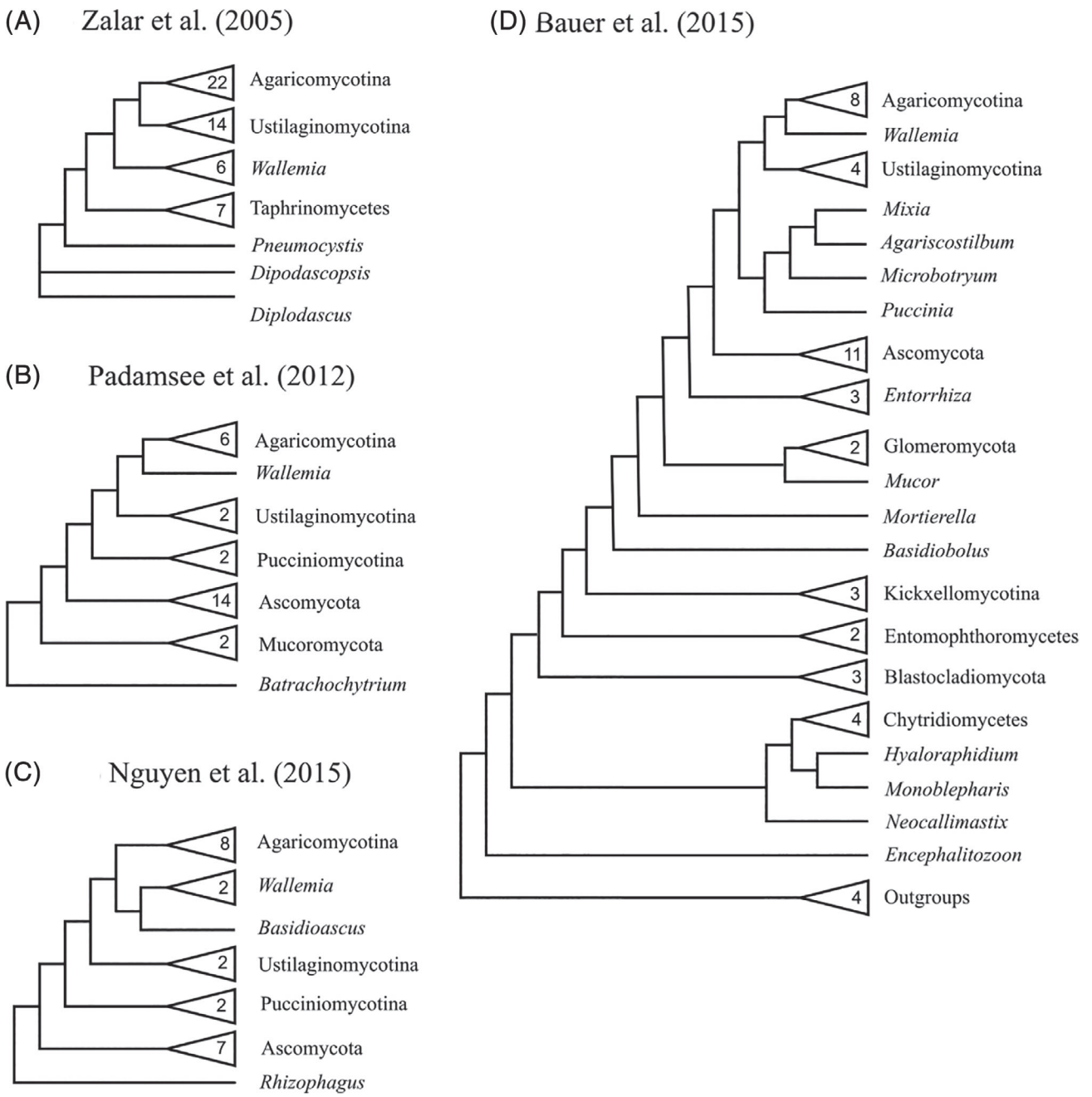

Fig. 7. Phylogenetic position of *Wallemia* in different studies. Simplified topology from several phylogenetic studies covering the phylogenetic position of Wallemiomycetes. Numbers inside triangles represent the number of sampled species within the clade. (A) Topology extracted from Zalar *et al.* (2005). Phylogeny constructed using a maximum-parsimony approach. (B) Topology extracted from Padamsee *et al.* (2012). Phylogeny constructed from a data set of 71 protein-coding genes, using a Bayesian inference approach. (C) Topology extracted from Nguyen *et al.* (2015). Pylogeny constructed from a data set of 35 single-copy protein-coding genes, using a Bayesian inference approach. (D) Topology extracted from Bauer *et al.* (2015). Phylogeny constructed from a concatenation of 18S rRNA, 28S rRNA, 5.8S rRNA, RPB1 and RPB2, using a combination of Bayesian inference, maximum-likelihood and maximum-parsimony approaches.

have highly complex life cycles (e.g. *Puccinia*) involving several hosts and free-living stages. Septal pores are simple, without dolipores. The cell wall contains mannose, but lacks xylose (Aime, Toome, & McLaughlin, 2014). Pucciniomycotina is generally considered the earliest-splitting lineage within the Basidiomycota, and consistent with this view they share some characteristics in their cell division and spindle-pole-body formation with the Ascomycota. Woronin body-like structures have been described in Agaricostilbomycetes and Cryptomycocolacomycetes (Aime *et al.*, 2014). Pucciniomycotina

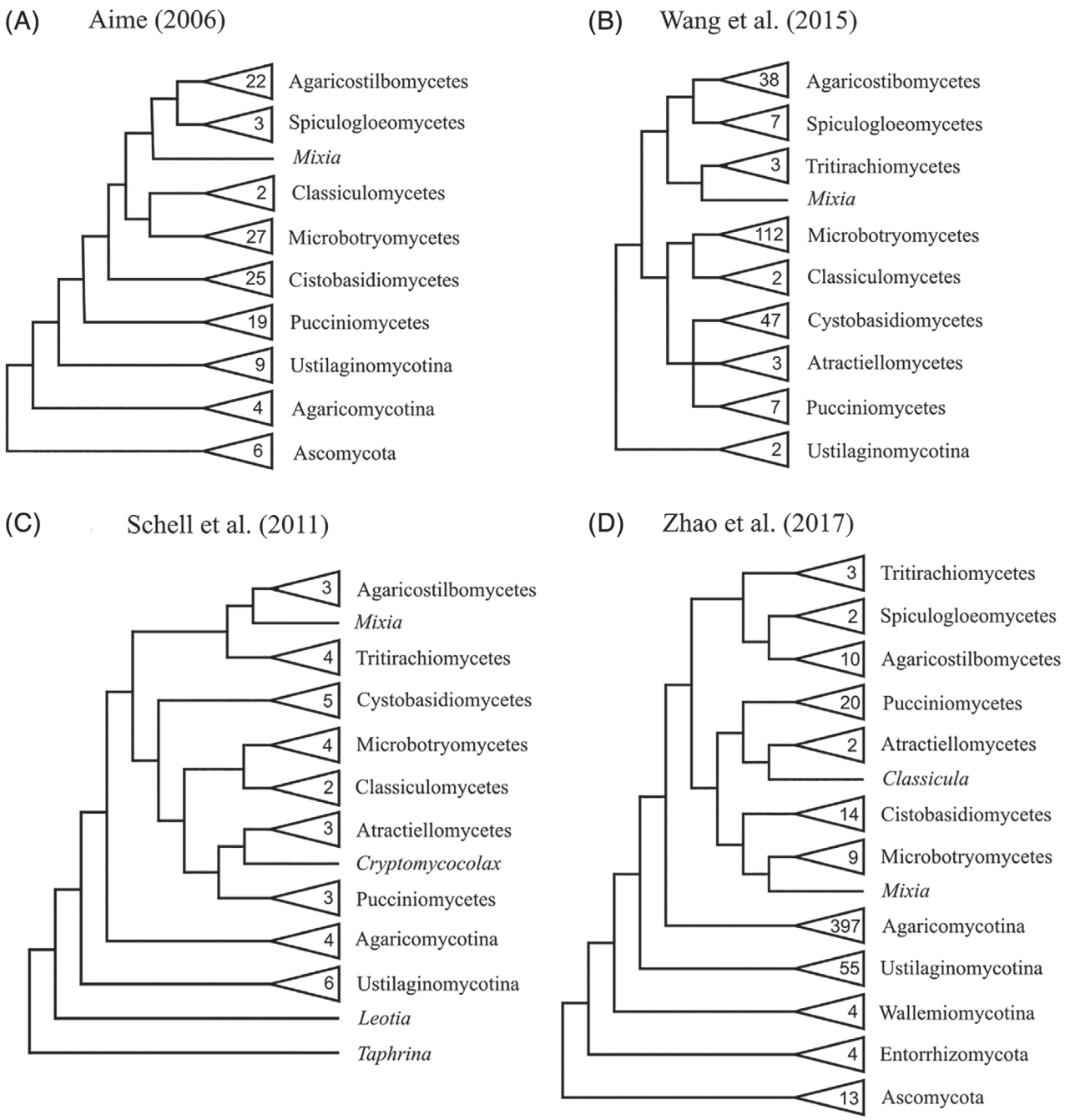

Fig. 8. Phylogenetic relationships among the different clades within Pucciniomycotina in different studies. Numbers inside triangles represent the number of sampled species within the clade. (A) Topology extracted from Aime *et al.* (2006). Phylogeny reconstructed from LSU rRNA and SSU rRNA genes, using a maximum-parsimony approach. (B) Topology extracted from Wang *et al.* (2015*c*). Phylogeny reconstructed from a concatenation of SSU rRNA and LSU rRNA D1/D2, using a maximum-likelihood approach. (C) Topology extracted from Schell *et al.* (2011). Phylogeny constructed from a concatenation of EF1-α, LSU rRNA and SSU rRNA genes, using a maximum-parsimony approach. (D) Topology extracted from Zhao *et al.* (2017). Phylogeny reconstructed from a concatenation of LSU rRNA, SSU rRNA, 5.8S rRNA, TEF1, RPB1 and RPB2, using a maximum-likelihood approach.

contains a widely diverse clade of mostly biotrophic plant pathogens called rusts (class Pucciniomycetes), as well as some free-living species that usually grow as a saprotrophic yeasts. Mycoparasites, insect pathogens and mycorrhizae are also described (Aime *et al.*, 2014). The relationship between the different classes of Pucciniomycotina is poorly resolved, with different phylogenetic studies producing highly contradictory results (Aime *et al.*, 2006; Schell *et al.*, 2011; Wang *et al.*, 2015*c*; Zhao *et al.*, 2017) (Fig. 8). Environmental studies suggest the existence of several undescribed major clades within

the subphylum (Tedersoo *et al.*, 2017), and taxonomists are fully aware that the lack of phenotypic characteristics of many of these fungi hides a wide diversity of cryptic species.

(*b*) *Ustilaginomycotina*

Ustilaginomycotina comprises around 1,700 species of mostly anamorphic or dimorphic yeasts. The majority of described species are plant pathogens, typically biotrophic (smuts), while others live as saprotrophic free-living yeasts or animal pathogens (e.g. *Malassezia*). Plant pathogens usually have asexual yeast states, often with saprobic capabilities, and an infecting dikaryotic mycelial stage (Begerow *et al.*, 2014). For most of the clades with only yeast forms, a sexual cycle has never been described (Begerow *et al.*, 2014; Wang *et al.*, 2015*a*). Septa are poreless and present a membrane cap or a true dolipore in some species of *Moniliella* (Moniliellomycetes) (Wang *et al.*, 2014). The group includes four classes: Ustilaginomycetes, Exobasidiomycetes, Malasseziomycetes and Moniliellomycetes, that span 10 orders, plus several *incertae sedis* genera (Begerow *et al.*, 2014). Some studies have raised doubts regarding the monophyly of Exobasidiomycetes (Hibbett *et al.*, 2007; Begerow *et al.*, 2014; Wang *et al.*, 2014), but so far they have been considered premature as grounds to reshape the taxonomy of the class.

(2) Agaricomycotina

Agaricomycotina is the largest group of Basidiomycota, containing around two-thirds of all described Basidiomycota. The subphylum includes three classes: Tremellomycetes, Dacrymycetes and Agaricomycetes (Hibbett *et al.*, 2007; Adl *et al.*, 2012, 2018), with Tremellomycetes the earliest-diverging clade. The Tremellomycetes include yeast species that can be dimorphic (e.g. *Cryptococcus*, *Tremella*, *Cystofilobasidium*), often forming macroscopic gelatinous fruiting bodies, although some species without a yeast stage are also known (Hibbett, 2006; Hibbett *et al.*, 2007; Adl *et al.*, 2012). Many species are mycoparasitic, living inside the fruiting bodies of other fungi and infecting them through a particular type of haustoria (tremelloid haustoria) (McLaughlin & Spatafora, 2014; Liu *et al.*, 2015). Others are free-living yeasts or animal pathogens. They present dolipores with endoplasmic reticulum projections (McLaughlin & Spatafora, 2014; Liu *et al.*, 2015). Five orders are recognized within the Tremellomycetes (McLaughlin & Spatafora, 2014). Many important genera in this group (e.g. *Cryptococcus*, *Tremella*) are paraphyletic (Liu *et al.*, 2015). The taxonomy of the group is currently highly volatile and many changes are expected in the near future.

The Dacrymycetes include a small group of wood-decaying fungi that produce gelatinous and usually highly pigmented fruting bodies. They are characterized by a unique basidial morphology (Hibbett, 2006; Shirouzu *et al.*, 2013, 2016). Shirouzu *et al.* (2013) described a second order, Unilacrymales, although its monophyly is questioned (Zhao *et al.*, 2017).

Agaricomycetes is by far the largest and most diverse class within the Agaricomycotina. The class comprises 22 orders and over 21,000 species (Shirouzu *et al.*, 2013; McLaughlin & Spatafora, 2014). Agaricomycetes possess dolipores, a trait shared with the Dacrymycetes (van Driel *et al.*, 2008, 2009; McLaughlin & Spatafora, 2014). The presence and structure of parenthesomes help define taxonomic groups. Mating-type loci systems can reach extreme levels of sophistication, with many species of mushrooms harbouring thousands of inter-compatible mating types (Kothe, 1996; Brown & Casselton, 2001; Raudaskoski & Kothe, 2010; Ni *et al.*, 2011; Coelho *et al.*, 2017). Many produce a high diversity of fruiting-body types whose morphologies have had traditional taxonomic value. Secondary metabolites are highly diverse in this group (Wisecaver, Slot, & Rokas, 2014; Wisecaver & Rokas, 2015).

Most agaricomycetes live as saprotrophs, plant pathogens or ectomycorrizae (McLaughlin & Spatafora, 2014; de Mattos-Shipley *et al.*, 2016). As for saprotrophs, many species are wood decaying, and are broadly classified as brown or white rots. White-rot fungi have developed a wide array of enzymes that allow them to degrade lignin, a metabolic feat unique to this group in the whole biosphere (Martínez *et al.*, 2005; Dashtban *et al.*, 2010; Floudas *et al.*, 2012; Sigoillot *et al.*, 2012; Riley *et al.*, 2014). Beyond these lifestyles, there are also nematode-trapping species (e.g. *Coprinus*, *Pleurotus*), insect symbionts (e.g. *Termitomyces*), lichens (e.g. *Dyctionema*), lichen-associated forms (e.g. *Burgella*), endophytes (e.g. *Piriformospora*), mycoparasites (e.g. *Pseudoboletus*) (McLaughlin & Spatafora, 2014) and amoebophagous species (e.g. *Pagidospora*, *Tulasnella*) (Duddington, 1956; Corsaro *et al.*, 2017). The phylogenetic backbone of Agaricomycetes is well resolved, at least to the order level (Hibbett, 2006; Zhao *et al.*, 2008, 2017). However, morphology-based identification of fruiting bodies hides a poorly explored pool of cryptospecies. Many species are discovered every year in undersampled areas and environmental studies (Zhao *et al.*, 2017), revealing an even greater hidden diversity of Agaricomycetes, particularly within early-diverging orders.

(3) Ascomycota

Ascomycota is the largest fungal phylum comprising roughly two-thirds of all described species (Lutzoni *et al.*, 2004; Schoch *et al.*, 2009; McLaughlin & Spatafora, 2015). The diversity of this group, combined with relative ease of experimental manipulation, has made Ascomycota the 'default' fungi. Certain species (e.g. *Saccharomyces cerevisiae*, *Neurospora crassa*, *Emericella nidulans*, *Schizosaccharomyces pombe*) have been used extensively as model organisms, for which extensive genetic studies have been performed and which have served to drive breakthrough discoveries in the field of biology. Mating induces the formation of dikaryon hyphae that, unlike in Basidiomycota, are normally very short lived. The dikaryon hypha leads to the formation of the ascus, a sac-like structure that contains the (usually eight) meiosis-derived spores. Asexual spores or other means of asexual propagation are very common, and sexual stages are unknown for many members of the phylum. Ascomycota

range from simple yeasts to fungi with highly complex macroscopic fruiting bodies. The phylum contains three main classes: Taphrinomycotina, Saccharomycotina and Pezizomycotina (Stajich *et al.*, 2009; Spatafora *et al.*, 2017*b*), with Saccharomycotina and Pezizomycotina being sister lineages. While environmental studies suggest the existence of a large amount of unknown diversity, all clades up to the class level have cultured or morphologically characterized reresentatives (Hibbett *et al.*, 2007; Adl *et al.*, 2012, 2018).

(*a*) *Taphrinomycotina*

The Taphrinomycotina (previously known as Archiascomycota) is a species-poor but physiologically diverse group of Ascomycota. It currently includes several genera spread over five classes: Taphrinomycetes includes eight genera of biotrophic plant pathogens (*Taphrina*, *Protomyces*) and saprotrophic yeasts (*Saitoella*) (Sugiyama, Hosaka, & Suh, 2006; Liu *et al.*, 2008*b*; Adl *et al.*, 2012; Spatafora *et al.*, 2017*b*); Neolectomycetes includes fruiting-body-forming species (*Neolecta*) of uncertain lifestyle and multicellular structures that have arisen independently to those found in Pezizomycotina or Agaricomycotina (Landvik *et al.*, 2003; Healy *et al.*, 2013; Nguyen *et al.*, 2017); Schizosaccharomycetes contain a single genus of saprotrophic yeasts (*Schizosaccharomyces*) that include the fission yeast *S. pombe*, an important model organism (Rhind *et al.*, 2011; Kurtzman & Sugiyama, 2015); Pneumocystidomycetes contain a genus of biotrophic lung parasites of mammals (*Pneumocystis*) (Sugiyama *et al.*, 2006; Hauser *et al.*, 2010; Porollo *et al.*, 2014); and Archaeorhizomycetes, with only two cultivated species of filamentous root endophytes in the genus *Archaeorhizomyces* (Rosling *et al.*, 2011; Menkis *et al.*, 2014). Archaeorhizomycetes was first described based on environmental sequences as a cosmopolitan and diverse clade of soil fungi termed the Soil Clone Group I (Porter *et al.*, 2008). Analyses in soil suggest they are at relatively low abundance and are probably associated with the rhizosphere (Porter *et al.*, 2008; Rosling *et al.*, 2011; Menkis *et al.*, 2014). At least one member of each described class of Taphrinomycotina has been sequenced, and so far all possess reduced and compact genomes. The monophyly of the group has been a matter of intense debate (Hibbett *et al.*, 2007; Liu *et al.*, 2008*b*; Ebersberger *et al.*, 2012; Menkis *et al.*, 2014; Ren *et al.*, 2016) mostly due to incongruences between mitochondrial and nuclear phylogenies and usually an unstable phylogenetic position of *Schizosaccharomyces* caused by its long branches. While the monophyly of Taphrinomycotina is well supported, the relationships among the different classes within the subphylum are still subject to debate (Liu *et al.*, 2008*b*; Ebersberger *et al.*, 2012; Kurtzman & Sugiyama, 2015). The only class within the group that is not monotypic, the Taphrinomycetes, might not be monophyletic, as the exact affiliation of *Saitoella* remains elusive.

(*b*) *Saccharomycotina*

Nearly all members of Saccharomycotina (previously known as Hemiascomycota) grow as yeasts, although many can switch to a filamentous form with varying degrees of complexity. Asci are typically formed inside the mother cell, surrounded by simple membranes (Hibbett *et al.*, 2007; Adl *et al.*, 2012, 2018). Many members of the Ascoideaceae, Cephaloascaceae, Endomycetaceae and Saccharomycetaceae are always filamentous (Deák & Péter, 2013). Filamentous forms contain septa with multiple micropores. Their genomes are highly streamlined and gene rich showing extensive gene loss and a great reduction of transposable elements and introns (Dujon *et al.*, 2004; Dujon, 2010; Dujon & Louis, 2017). Most lineages present only one ribosomal DNA (rDNA) locus that contain tens or hundreds of copies in tandem and which usually contains the 5S rRNA loci (Proux-Wéra, Byrne, & Wolfe, 2013; Dujon & Louis, 2017). Several lineages have deviations from the canonical genetic code that affect sense codons (Sugita & Nakase, 1999; Mühlhausen & Kollmar, 2014; Mühlhausen *et al.*, 2016). Sex is well studied within this group, and many examples of hybrids exist in nature and under laboratory conditions (Morales & Dujon, 2012; Ga *et al.*, 2013; Hittinger *et al.*, 2015*a*; Mixão & Gabaldón, 2018).

Saccharomycotina is, by far, the best represented eukaryotic lineage in terms of genomic information. *Saccharomyces cerevisiae* was the first sequenced eukaryote (Goffeau *et al.*, 1996) and about 10% of the described Saccharomycotina have now been sequenced (Dujon & Louis, 2017). In stark contrast with our understanding of their physiology, biochemistry, genetics and evolution, our knowledge about the ecology of this group is fairly limited (Kurtzman & Sugiyama, 2015; Treseder & Lennon, 2015; Hittinger *et al.*, 2015*a*; Shen *et al.*, 2016; Dujon & Louis, 2017). Many species seem to associate with certain microniches, such as animal mucosae, animal gut, flowers, fruits or trees, while others are *bona fide* plant pathogens (e.g. *Eremothecium*). Several species are adapted to extreme environments, including growth at high osmotic pressure, high temperature, high carbon dioxide concentration, in the presence of toxic compounds or on unusual carbon sources. Most species are unable to exploit complex polysaccarides, and metabolic clusters for the production of complex secondary metabolites (e.g. alkaloids, polyketides or non-ribosomal peptides) are practically non-existent. Genomic data in the last two decades has allowed us to tackle the problematic phylogeny and taxonomy of yeasts, which are devoid of phenotypic traits (Dujon *et al.*, 2004; Wolfe, 2006; Dujon, 2010; Mühlhausen & Kollmar, 2014; Hittinger *et al.*, 2015*b*; Shen *et al.*, 2016; Dujon & Louis, 2017). This has proved the paraphyly of certain important genera (e.g. *Candida*, *Pichia*), currently undergoing nomenclatural redefinition from established names with decades of usage to newer ones based on phylogenetic evidence. Currently, Saccharomycotina is circumscribed into a single class and order (Saccharomycetes, Saccharomycetales), spanning 14 families and around 1500 species (Kurtzman, Fell, & Boekhout, 2011).

(*c*) *Pezizomycotina*

Pezizomycotina (previously known as Euascomycota) is the most diverse subphylum of Ascomycota. The basic body

plan of this subphylum is filamentous and anastomosed, with septa that present a peroxisome-derived electrodense organelle called the Woronin body (Liu *et al.*, 2008*a*; Adl *et al.*, 2012; Healy *et al.*, 2013). Asci are typically protected and supported by multicellular structures named ascocarps or ascomata. Some members are unicellular. Comparative genomics has revealed a unique mode of genome evolution termed mesosynteny, in which genomic regions mantain a conserved gene content without conservation of the gene order. Mesosynteny has only been described in pezizomycotina, and seems to be particularly strong in members of the Dothideomycetes (Hane *et al.*, 2011). Compared to other fungi, they tend to contain a high abundance of enzymes for secondary metabolism (Wisecaver *et al.*, 2014; Wisecaver & Rokas, 2015). Pezizomycotina are currently circumscribed into 67 orders in 13 classes (Hibbett *et al.*, 2007; Adl *et al.*, 2012, 2018; Gazis *et al.*, 2012; Spatafora *et al.*, 2017*b*): Arthoniomycetes, Coniocybomycetes, Dothideomycetes, Eurotiomycetes, Geoglossomycetes, Laboulbeniomycetes, Lecanoromycetes, Leothiomycetes, Lichinomycetes, Orbiliomycetes, Pezizomycetes, Sordariomycetes and Xylonomycetes. An important fraction of Pezizomycotina remains unclassified. For instance, the Catalogue of Life (Bisby & Rosko, 2010, accession date June 2019) contains more than 5000 species whose affiliation to any of these classes is unknown, many not even assigned to a family level.

Their living strategies vary wildly, but special mention must be made of lichenized Pezizomycotina. Approximately 40% of the group are lichens and around 98% of lichens are Pezizomycotina. Since lichens form macroscopic thalli with well-defined morphological traits, the amount of lichen hidden diversity is probably lower than for other types of Ascomycota. A lichenic lifestyle appears in six classes (Grube & Wedin, 2016), and for the classes Arthoniomycetes, Coniocybomycetes, Lichinomycetes and Lecanoromycetes only lichenic species are known. Most non-lichenic members of the Pezizomycotina have saprobic capabilities to a certain degree, although more-specialized facultative lifestyles are common. Many are mycorrhizal, plant pathogens, endophytes, animal parasites and symbionts, mycoparasites, amoebophagous, endolichenic or endolythic (Stajich *et al.*, 2009; Corsaro *et al.*, 2017; Spatafora *et al.*, 2017*b*).

V. FUNGI INCERTAE SEDIS

We here discuss some groups whose classification, even to the level of broad taxonomic affiliation, remains elusive. See Table 6 for a list of these groups.

(1) Early-splitting environmental lineages

The use of metabarcoding approaches, mostly using ribosomal RNA (rRNA) genes, has revealed the existence of several deep branches in the fungal tree of life for which we still do not have any cultured representative. Enviromental studies have identified two early-diverging and relatively diverse clades of fungi termed the Basal Clone Group 1 (BCG1) (Nagahama *et al.*, 2011; Tedersoo *et al.*, 2018) and BCG2 (Monchy *et al.*, 2011; Tedersoo *et al.*, 2017, 2018; Bass *et al.*, 2018). BCG1 is a marine clade that appears related to Rozellidea, and thus it could be considered a novel lineage within the Opisthosporidia. BCG2 on the other hand, has been detected from soils and fresh water, and might be the sister group to all non-Opisthosporidia Fungi. Finally, the environmental clade Namako-37 is an unexplored lineage related to Rozellidea and Microsporidia (Takishita *et al.*, 2007; Bass *et al.*, 2018). The identification and study of these groups would provide invaluable information about the origin and early evolution of Fungi.

(2) Nephridiophagida

Nephridiophagida is an enigmatic and understudied group of intracellular parasites historically classified as related to Haplosporidia or Microsporidia, to the point that some species were originally described within microsporidian genera (Radek *et al.*, 2017). To date, members of this group have been only described as extracellular parasites associated with the Malpighian tubules of some insects and the millipede *Xenobolus*. Four genera are currently described: *Nephridiophaga*, *Coelosporidium*, *Oryctospora* and *Peltomyces* (Lange, 1993; Radek *et al.*, 2017). *Nephridiophaga periplanetae* has been described as a multinucleated mitochondriated amoeboid stage with the ability to attach to microvilli of the host cell and with endocytic germination with somatic and germinative differentiation of nuclei (Lange, 1993; Radek *et al.*, 2017). The first phylogenetic analysis of this group based on the 18S rRNA gene placed them within zygomycetous fungi, and they have been proposed to be related to Dimargaritales or Harpellales (Wylezich, Radek, & Schlegel, 2004). A second analysis using small subunit (SSU) rRNA genes returned an affiliation with Chytridiomycota, albeit with low support (Radek *et al.*, 2017).

(3) Zoosporic fungi *incertae sedis*

The phylogenetic positioning of several chytrid-like lineages is highly debated. *Olpidium* is a morphologically reduced obligate biotrophic plant pathogen (Powell & Letcher, 2014), which makes it relatively difficult to study. Its lifestyle has likely shaped its genome, making it susceptible to phylogenetic artefacts (James *et al.*, 2006*b*; Sekimoto *et al.*, 2011). *Caulochytrium* is an enigmatic parasite of other fungi that presents aerial sporangia, a unique trait within the Chytridiomycota (Olive, 1980). Its phylogenetic position has not been studied, although a relationship with *Olpidium* has been proposed based on the structural characteristics of their zoospores. The algal parasites *Sanchytrium* and *Amoeboradix* were recovered as a divergent lineage based on ribosomal rRNA phylogenies (Karpov *et al.*, 2017*a*, 2018). These two organisms are united by the presence of amoeboid zoospores. Several groups of uncultured chytrids have been described from environmental studies that seem to stem from different points of the chytrid tree of life (Richards *et al.*,

Table 6. Fungi *incertae sedis* and environmental taxa. Due to changes in the scope of certain historical clades, references might not refer to the initial published description of a clade but to more recent bibliography

Name	Main described lifestyles	Main traits	Representative genera	Main phylogenetic hypotheses
NCLC1 (also known as Basal Clone Group 1) (Richards *et al.*, 2015, 2017; Bass *et al.*, 2018)	Unknown, detected in marine environments	Unknown	None described	Probable sister lineage to Rozellidea + Microsporidia
Basal Clone Group 2 (also known as GS01) (Monchy *et al.*, 2011; Tedersoo *et al.*, 2017, 2018; Bass *et al.*, 2018)	Unknown, detected in soil and freshwater environments	Unknown	None described	Probable sister lineage to all Fungi
Namako-37 (Takishita *et al.*, 2007; Bass *et al.*, 2018)	Unknown, first detected in anoxic sediments from a lake	Unknown	None described	Distinct lineage within Rozellidea or Microsporidia; branches closer to traditional Microsporidia than to Rozella; might rise as a novel high-level taxon after revision of Opisthosporidian taxonomy
Nephridiophagida (Lange, 1993)	Extracellular parasites in the nephridia of certain arthropods	Multicellular plasmodia; endocytic germination with nuclear functional differentiation	*Nephridiophaga*	Fungi *incertae sedis*; all evidence suggests they are members of Eumycota
Amoeboradix + *Sanchytrium* (Karpov *et al.*, 2018)	Algal parasitoids	Amoeboid zoospores; large kinetosome	*Amoeboradix*, *Sanchytrium*	Fungi *incertae sedis*
Olpidiaceae (Tedersoo *et al.*, 2018)	Biotrophic plant pathogens	Zoosporic, single flagellum; thallus monocentric, holocarpic or eucarpic; two parallel centrioles linked to nucleus by shared, tapering, striated rhizoplast; porangium single, endobiotic	*Olpidium*, *Cibdelia*	Independent lineage of zoosporic fungi; early phylogenies clustered them with Zoopagomycota; most modern phylogenies recover them as sister to terrestrial fungi
GS19 (Tedersoo *et al.*, 2017)	Unknown, detected from soil	Unknown	None described	Falls within Zoopagomycota, either as a novel lineage or as an unexplored lineage within Kickxellomycotina
Caulochytrium (Voos, 1969; Olive, 1980)	Mycoparasite	Presence of aerial sporangia; monocentric thallus and eucarpic, presence of rhizoids	*Caulochytrium*	Probably related to *Olpidium*
Nothadelphia (Degawa & Gams, 2004)	Mycoparasite	Haustorial parasite; mycelium irregularly septated and scarcely branched; absence of collumella; sporangia leave a minute collarette after dequiescence	*Nothadelphia*	Proposed as a member of the Mortierellomycotina; no phylogenetic studies are available
Calcarisporiella + *Echinochlamydosporium* (Tedersoo *et al.*, 2018)	Saprobes, nematophagous	Thallus branched and septate; thin-walled hyphae; simple sporangiophores; globose, spiny chlamydospores borne laterally on short hyphae	*Calcarisporiella*, *Echinochlamydosporium*	Distinct lineage branching sister to Mucoromycotina; formerly classified as members of Mortierellomycotina; Tedersoo *et al.* (2018) elevated them to the subphylum Calcarisporiellomycotina
Densosporaceae (McGee, 1996; Desirò *et al.*, 2017)	Ectomycorrhizal	Sporocarps hypogeal, with numerous small blastospores; blastospores globose, terminal or intercalary, developed on thin hyphae, with the lumen of the hyphal appendages completely occluded; in some mature blastospores, wall irregularly thickened and lumen deformed; blastospores with thickened walls often deformed and contents viscid	*Densospora*, *Sphaerocreas*	Morphological characteristics suggest ambiguous affiliation to either Mucoromycotina or Glomeromycotina; Desirò *et al.* (2017) recovered it as an independent lineage related to Endogonales
Bifiguratus (Torres-Cruz *et al.*, 2017)	Soilborne or endophyte in mosses; living in association with a wide array of bacteria; dimorphic	Coenocytic hyphae with ornamentations; intercalary and terminal chlamydospores; no sporangia observed to date	*Bifiguratus*	Torres-Cruz *et al.* (2017) recovered it as an early-splitting lineage within Mucoromycotina
Entorrhizomycota (Bauer *et al.*, 2015) syn. Entorrhizomycotina within Basidiomycota	Root-associated endophytes	Presence of basidia; forms intracellular septate hyphal coils	*Entorrhiza*, *Talbotiomyces*	Bauer *et al.* (2015) recovered it as sister to the rest of Basidiomycota or the rest of Dikarya and proposed elevation to phylum Entorhizomycota; Zhao *et al.* (2017) and Tedersoo *et al.* (2018) recovered it as sister to Basidiomycota and retained the phylum level

2015; Tedersoo *et al.*, 2017). Of particular interest are soil clades GS17 and GS18, which are related to *Olpidium*. The phylogenetic peculiarities of *Olpidium* and several related plant-pathogenic genera have led to the recent creation of a new phylum Olpidiomycota to accommodate them (Tedersoo *et al.*, 2018). Future phylogenetic work should aim to address the relationship of *Olpidium* with other fungi in order to establish the position and boundaries of this nascent phylum.

(4) Zygomycetous fungi *incertae sedis*

A few zygomycetous fungi currently hold an uncertain phylogenetic affinity, particularly in the Mucoromycotina, Mortierellomycotina and Glomeromycota. Recent phylogenetic studies based on 18S rRNA place the genus *Sphaerocreas* as a sister branch to a group of uncultured symbionts of liverworts, forming a distinct lineage within Mucoromycotina (Hirose *et al.*, 2014; Benny *et al.*, 2016). *Densospora* (McGee, 1996) is an ectomycorrhizal fungus isolated from Australia that contains several morphological traits that suggest ambiguous affiliation to either Endogonales or Glomeromycota (Gleason & McGee, 2004; Desirò *et al.*, 2017). A multigene phylogeny recovered an affiliation between *Sphaerocreas* and *Densospora* – a relationship that should further be explored in the near future (Desirò *et al.*, 2017). *Bifiguratus* is a recently described fungus with an endophytic and saprotrophic lifestyle that appears as a distinct and early-splitting lineage within the Mucoromycotina (Torres-Cruz *et al.*, 2017). *Calcarisporiella* was traditionally classified as an Ascomycota, and was recently shown to form a distinct lineage in an uncertain position within Mucoromycota (Hirose *et al.*, 2012), and related to *Echinochlamydosporium* (Hirose *et al.*, 2014). Due to the position of these lineages, it is very likely that mycologists will erect higher-level taxonomic categories to accommodate them once their phylogenetic position has been determined with precision. Finally, *Nothadelphia* is an unplaced biotrophic parasite of *Mortierella* (Degawa & Gams, 2004). The description of *Nothadelphia* suggest similarities with mycotrophic chytrids, but the authors classified it as Zygomycota *incertae sedis* due to its apparent inability to form zoospores, suggesting a possible affiliation with Mortierellomycotina.

(5) Entorhizomycota

The genus *Entorrhiza* contains about a dozen species that are associated with the roots of members of Cyperaceae and Juncaceae (Bauer *et al.*, 2015; Riess *et al.*, 2015). *Talbotiomyces* is another root endophyte isolated as root galls in several families of Caryophyllales (Vánky, Bauer, & Begerow, 2007). The phylogenetic placement of *Entorrhiza* has been historically controversial, being variously placed as a distinct lineage of Ustilagomycotina (Bauer, Oberwinkler, & Vánky, 1997; Begerow, Stoll, & Bauer, 2006) or as a member of Tremellomycetes or Pucciniomycotina (Vánky *et al.*, 2007). Recent phylogenetic analyses of *Entorrhiza* placed it as either sister to the rest of Basidiomycota or as sister to the rest of Dikarya, for which the authors proposed elevation to phylum level (Bauer *et al.*, 2015); while a six-gene phylogeny recovered them with high support as the sister branch to all Basidiomycota (Zhao *et al.*, 2017). The classical relationship between *Talbotiomyces* and *Entorrhiza* based on morphological traits (Vánky *et al.*, 2007) was recently confirmed by molecular phylogenies, and the order Talbotiomycetales was proposed (Riess *et al.*, 2015). Environmental studies do not suggest the existence of a wide undescribed diversity of Entorrhizomycota, but novel genera associated with the roots of unsampled plants are to be expected (Tedersoo *et al.*, 2017).

VI. CONCLUDING REMARKS

The Fungi is a fascinating group of organisms entailing a vast diversity that have important roles in virtually all ecosystems. The answer to the question 'what is a fungus' does not have a simple answer.

Fungi started as unicellular, flagellated, eukaryvorous organisms. This lifestyle is still prevalent in the zoosporic lineages and implies a series of traits that are ancestral to the Kingdom. Elucidating the phylogenetic relationships among the zoosporic lineages and describing the 'fungal dark matter' is essential for our understanding of this group in a broad sense. The morphological and genomic reduction associated with a parasitic lifestyle makes it even more difficult to reconstruct the ancestral state of the different fungal lineages, or to find common features among the modern lineages. Most well-studied fungi are terrestrial. This group represents a highly derived lifestyle that has been incredibly successful. The large number of described species in this lineage, together with their prevalence in terrestrial environments and the possession of well-defined, widespread and ancestral morphological and biochemical traits has spawned a thriving academic community with more than a century of history. This in turn has led to the biased view that considers terrestrial fungi as representing the canonical fungal identity, while zoosporic lineages are regarded as evolutionary stepping stones towards that presumed ideal. While no serious evolutionary biologist will recognize this view as scientifically valid, it still permeates and conditions our collective view of the Fungi. The search for synapomorphies to unify the Fungi has failed (Richards *et al.*, 2017) and we must get used to this lack of hard taxonomic boundaries. More important, in our view, is to understand what evolutionary transitions define the main fungal lineages and how they relate to their particular adaptations.

The phylogenetic backbone of fungi has steadily grown more and more solid as genomic information has accumulated during the last decade. Such information has confirmed the monophyly of the Ascomycota and Basidiomycota and the delimitations of their main subphyla, recognized the phylogenetic identity of the Blastocladiomycota, and turned the disorganized assemblage of orders that were the 'Zygomycota' into a defined set of phylogenetic lineages. From single-gene-based phylogenetic

approaches we have moved to full phylogenomic studies that have helped to resolve some of the most intractable evolutionary puzzles in the group, such as the placement of Microsporidia and the relationships among the different clades within the zygomycetous fungi. Environmental sequencing has provided us with new and exciting prospects in fungal taxonomy, with the description of the Cryptomycota and the Archaeorrhizomycetes as two highly diverse and virtually uncultured taxa with an important presence in the environment. Such studies suggest that most major lineages of Fungi contain species described through traditional means (Tedersoo *et al.*, 2017). However, this does not imply that we possess an adequate understanding of fungal diversity, which remains very unevenly explored and is reflected in the taxonomy of the different clades that form the kingdom. For instance, information on sequence divergence of different species of *Schizosaccharomyces* (Taphrinomycotina) (Rhind *et al.*, 2011; Naumov, Kondratieva, & Naumova, 2015) or *Rozella* (Rozellomycota) (Gleason *et al.*, 2012) should allow us to split those genera, likely raising new higher taxonomic ranks. However, in the absence of information regarding existing genetic and physiological diversity within these groups, a proper taxonomic revision is still not possible. This is particularly urgent for *Schizosaccharomyces*, given its wide use as an experimental model.

We live in a time of transition for fungal taxonomy, as we continue to characterize new fungal diversity but struggle to provide a coherent and unified framework. The next few decades will bring an avalanche of information from several early-diverging lineages, data that might imply a re-evaluation of at least some of the main groups discussed herein. Such is the case for the Microsporidia and Rozellidea, which very likely will be merged, for uncultured deep-branching lineages of Chytridiomycota and other zoosporic fungi, such as *Olpidium* and associated sequences or novel environmental lineages, for which we still lack even a basic phylogeny, for the GS19 clade within the Zoopagomycota, for the Endogonales and the genera *Densospora*, *Nothadelphia*, *Calcarisporiella* and Echinochlamydosporium within the boundaries of Mucoromycotina, Mortierellomycotina and Glomeromycota, and for the genera *Entorrhiza* and *Talbotiomyces* at the base of Basidiomycota. The placement of some other groups is yet to be investigated, including BCG1 and BCG2, the Nephridiophagida, and the Meristacraceae. Solving these relationships satisfactorily will surely produce great taxonomic revisions. In this regard, a recent work (Tedersoo *et al.*, 2018) proposed the use of a diverged-time-based approach to fungal taxonomy and, together with rRNA phylogenetics, supports a radical nomenclatural shift that we must reject at present, at least in broad terms. While we understand and value their proposed strategy, we advise caution regarding the robustness of their phylogenetic results and consider that several of their new taxonomic proposals introduce unnecessary changes in otherwise well-established taxa. Because of this, we herein adopted a more orthodox and conservative taxonomic approach, prioritizing the use of older names in cases where the phylogenetic delineation of the taxa is volatile and attempting to use naming conventions that are consistent with the main phylogenetically conflicting topologies when possible. Environmental sampling is also increasing our understanding of the sister groups of Fungi, holding the promise of expanding our knowledge of the evolution of not just Fungi, but of Opisthokonta in particular and of Eukaryotes in general.

VII. CONCLUSIONS

(1) Solving the phylogenetic relationships among the zoosporic fungi is an on-going challenge. Genomic sampling in these lineages is still poor, many are plagued with long branches due to their parasitic lifestyle, and environmental sequences suggest the existence of a large unsampled diversity within these groups.

(2) By contrast, recent studies have produce great advances in our knowledge regarding the relationships among the main lineages of zygomycetous fungi. However, several lineages are still to be placed. In particular, the boundaries between Mucoromycotina, Mortierellomyctina and the Glomeromycotina seem to contain several poorly studied groups that will force re-evaluation of the phylogenetic relationships among these groups.

(3) Both Basidiomycota and Ascomycota have suffered recent drastic taxonomic revisions that have affected primarily the Pucciniomycotina, Agaricomycotina and the Pezizomycotina. The phylogeny of both groups is fairly well resolved and environmental data suggest that there are no major (at least to a class level) unsampled lineages. The phylogenetic placement of certain lineages of Basidiomycota is still controversial (*Bartheletia*, Wallemiomycetes). Ascomycota, on the other hand, contains many poorly studied low-rank taxa whose position is unknown and for which sequence data are still unavailable.

(4) Several lineages have not yet been assigned robustly to any of the known phyla, some of which might be erected as novel phylum-level clades in the near future. Herein we highlight the Nephridiophagida, a poorly studied group of arthropod parasites that appear in two phylogenetic works as *bona fide* fungi but have been largely ignored by mycologists.

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